Removal Rates of Native and Exotic Dung by Dung Beetles (Scarabaeidae: Scarabaeinae) in a Fragmented Tropical Rain Forest

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Environ. Entomol. 39(2): 328–336 (2010); DOI: 10.1603/EN09182

ABSTRACT Many studies have evaluated the effect of forest fragmentation on dung beetle assemblage structure. However, few have analyzed how forest fragmentation affects the processes carried out by these insects in tropical forests where their food sources consist mainly of dung produced by native herbivore mammals. With the conversion of forests to pastures, cattle dung has become an exotic alternative and abundant food for dung beetles. This study compares dung removal rates of native (monkey) and exotic (cow) dung in different-sized fragments of tropical rain forests, during the dry and rainy seasons at the Los Tuxtlas Biosphere Reserve. Dung removal rates were affected by season, dung type, and the interaction between resource type and season. During the dry season, the removal rates of monkey dung were somewhat similar than during the rainy season, whereas the removal rates of cow dung were much higher during the rainy season. Dung beetle biomass and species richness were almost three times greater in monkey dung than in cow dung. Monkey dung attracted species belonging to the dweller, roller, and tunneler guilds; cow dung attracted mostly tunnelers. Therefore, the use of exotic dung may result in a biased misconception of the rates of dung removal in tropical forest and an underestimation of dung beetle diversity. This study highlights the importance of working with natural tropical forest resources when attempting to identify realistic tendencies concerning processes in natural habitats and those modified by fragmentation and by other human activities.

KEY WORDS dung beetles, dung removal, forest fragments, biomass, monkey and cow dung

Forest fragmentation and habitat loss, the main causes driving changes in the distribution and abundance of organisms, can generate modifications in ecological processes such as nutrient cycling, seed dispersal, and pollination (Wilcox and Murphy 1985, Laurance et al. 2000, Andresen 2003, Nichols et al. 2008). Much research has focused on analyzing the effects of forest fragmentation on community structure, but little is known about its effects on ecological processes (Saunders et al. 1991, Andresen 2003, Vulinec 2002, Gardner et al. 2008). Understanding ecological processes allows recognition of the range of environmental services provided by ecosystems as a whole and by the guilds or individual organisms that are directly or indirectly beneficial to humans (Andresen 2003; Nichols et al. 2007, 2008; Aguirre and Dirzo 2008).

Removal rates of seeds and pollination have been studied in tropical ecosystems for different animal groups, including mammals (Forget 1996, Beck and Terborgh 2002), birds (Weeny 2000, Carlo and Morales 2008), and insects (Hughes and Westoby 1990, Vander Wall et al. 2005, Freymann et al. 2008). Some studies have addressed the effect of fragmentation on seed dispersal and on pollination resulting from the loss of birds, aerial and terrestrial mammals, and some primates, which may be related to the reduction of plant regeneration (Andresen 1999, Medellin and Gaona 1999, Cramer et al. 2007). Various insect species such as ants, termites, and particularly dung beetles (Scarabaeidae: Scarabaeinae) remove the dung of mammals and other animals in tropical forests. Dung beetles are crucial for maintaining the functions and services of the ecosystem (Nichols et al. 2007, 2008). Dung removal is a crucial step in the process of nutrient cycling because it helps with soil fertilization and soil aeration; it accelerates mineralization rates, increases soil nutrients, and contributes to pest control and seed dispersal.

Scarabaeinae dung beetles are an excellent focal taxon for analyzing the effect of anthropogenic disturbance on community structure in tropical terrestrial environments (Favila and Halffter 1997, Spector 2006). During the 2008 ScarabNet (The Scarabaeinae Research Network) meeting, members concluded that the comparative analysis of the dung removal rates by Scarabaeinae dung beetles in tropical forest fragments is one of the most important research goals for the next few years. Several studies have evaluated the percentage and speed of cattle dung removal by

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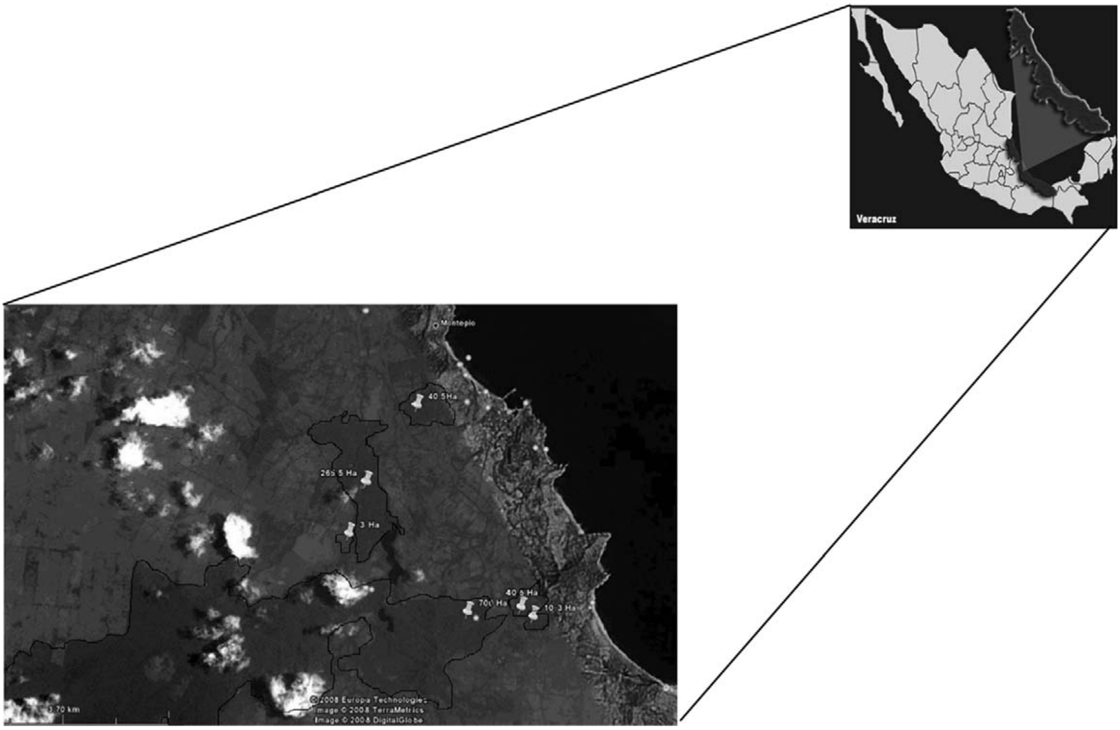

Fig. 1. Study sites in Los Tuxtlas, Veracruz, Mexico.

dung beetles in pastures (Horgan 2002, Anduaga 2004). Interestingly, the few studies that analyze dung removal rates in tropical forests have been done using introduced herbivore dung, mostly cow dung (Klein 1989; Horgan 2005, 2008; Slade et al. 2007, but see Andresen 2003). To properly understand and by accurately evaluate the effects of forest fragmentation on dung removal rates as a preliminary step in nutrient cycling requires the use of native dung, even though, for practical reasons, cow dung may be easier to obtain.

In this study, we compare removal rates for native (monkey) and exotic dung (cow dung) by forest dung beetles in fragments of different size during the dry and the rainy season in the Los Tuxtlas region of Mexico. Our predictions were that (1) the rate of native dung removal would be higher than those of exotic dung, (2) such differences would be caused by differences in dung beetle biomass and guild structure on the two types of dung, (3) the rate of dung removal by dung beetles in forest fragments should increase with fragment size, and (4) dung removal rates are greater during the rainy (reproductive) season.

Materials and Methods

Study Area. Field work was conducted at the Los Tuxtlas Biosphere Reserve, located in the southeastern part of Veracruz State, at 95°04′ W and 18°34′ N. This region represents the northernmost limit of the tropical rain forest in Mexico (Dirzo and Miranda 1991). The area is dominated by tropical rain forest vegetation with a mixture of cloud forest and conifers at higher elevations (Mendoza et al. 2005, Aguirre and Dirzo 2008). Annual rainfall ranges from 3,000 to 4,500 mm, and mean annual temperature is 24–26°C. The dry season occurs from March to May, with 111.7 mm of rain per month, and the rainy season occurs from June to February with a mean monthly rainfall of 486.25 mm (Soto 2004). In recent decades, much of Los Tuxtlas has been transformed from primary forest to pastures or crops, resulting in modified soil cover and landscape structure. Deforestation rates between 1960 and 1980 were estimated at 4–5% per year, and as a result of such intense disturbance, the landscape is dominated by relatively isolated forest fragments of different sizes (Dirzo and Garcia 1992).

Six forest fragments differing in size were selected using satellite images and field inspection. Size and isolation distances among fragments were estimated using ARCVIEW and later confirmed in the field. The selected fragments were (1) 3.0-, (2) 10.3-, (3) 40.5-, (4) 112.0-, and (5) 265.5-ha fragment and (6) 700 ha of continuous undisturbed forest (Fig. 1). The percentage of vegetation cover for each fragment was measured using a field densitometer that measures forest overstory density from unobstructed sighting positions and uses a spherical mirror engraved with a grid of 24 by 0.25-in squares. Percentage vegetation cover varied among fragments between 77 and 80% regardless of fragment size. Vegetation composition was similar for the fragments studied, with a predominance of original forest species such as *Astrocaryum mexicanum* Liebmann and secondary forest vegetation. The most abundant plant species in fragments were *Cymbopetalum baillonii* R.E. Fries, *Ficus perforata* L., *Poulsenia armata* (Miq.) Standl, *Pseudolmedia* sp., *Psychotria chiapensis* Standl., and *Swartzia guatemalensis* (Donn. Sm.) Pittier.

Field Work. Field work was conducted during 2007. Experiments were carried out during two separate periods: the first during the dry season, from 14 to 20 May, and the second during the rainy season, from 20 to 27 August. During each of the two periods, three containers with spider monkey (*Ateles geoffroyi* Khul 1820) dung, named here as monkey dung, and three with cow dung were set in each fragment. Monkey dung was obtained from a local zoo in Los Tuxtlas, where monkeys are fed with fruit from trees of the region, and from the Banderilla zoo near Xalapa, where monkeys are fed with *Ficus yoponensis* Desvaux, one of the most important tree species in Los Tuxtlas because it provides food for many frugivorous species, including spider monkeys. Cow dung was obtained from neighboring pastures. Monkey dung from both zoos was mixed before being placed in the traps.

Following the suggestions made by Larsen and Forsyth (2005), the containers were placed at the center of each forest fragment to minimize edge effects and set at least 50 m apart from each other to avoid interference. Traps were set at random in fragments in two lines of three (because in some cases fragment size did not allow setting of a continuous line). Each container consisted of a 17-cm-diameter by 17-cm-high plastic cylinder filled to three fourths of its capacity with soil, buried at ground level, baited with 200 g of dung (monkey or cow) placed over the soil within the trap, and covered with a plastic plate to avoid flooding in case of rain.

Decrease in dung weight because of dung beetle removal was measured with a ±0.01 g precision wire scale every 24 h over 96 h, after which the dung begin to lose its attractiveness (Howden and Nealis 1975). After weighing, the remaining dung was again placed in its container and checked 24 h later. At the end of the 96-h period, all containers were removed from the fragments. As a control for loss of weight by dehydration, cow and monkey dung was placed in containers identical to those described above, but covered with mesh to prevent dung beetle activity. These were also weighed every 24 h over 96 h.

The dung beetles collected were counted for each trap and identified to species level. Voucher specimens of the beetles were deposited in the collection of the Department of Biodiversity and Animal Ecology, Instituto de Ecologia, A.C. For each species, the biomass of its individuals was obtained by drying 10 beetles at 120°C for 48 h, after which they were weighed, and an average individual mass for each species was obtained. The total biomass of the beetles caught in each trap was calculated for each habitat and season by multiplying the abundance of each species present in a trap by the average biomass per individual for that species and adding the resulting values. Each individual was also measured with a ±0.003-mm precision digital caliper. All species captured were classified according to their food relocation behavior (dwellers, tunnelers, and rollers) and habitat preferences using species lists for Los Tuxtlas by Favila (2005) and Favila and Díaz (1997).

Data Analysis. Linear mixed effects models (lme) use a mixture of fixed effects and random effects as explanatory variables (Crawley 2004). The random effects in the lme are not estimated as part of the model, but it is possible to predict the values of the random effects once the model has been estimated (Everitt 2005). To analyze the effect of fragment size (six fragments of different sizes), resource type (monkey and cow dung), and season (dry and rainy) on dung removal rates over time (24 through 96 h), a linear mixed effects model (lme) with repeated measures over time (H) was constructed. Fragment size (F), resource type (R), and season (S) were set as fixed effects. Time (H) was considered a temporal random effect. Repeated measures in time were made for each trap in each of the fragments so we calculated the effect of the random effects (repeated measures in time [H], over traps nested in fragments) on dung removal rates.

To compare total dung beetle biomass after 96 h (a single sample at the end of the 96-h period), a linear model (lm) was constructed with biomass (*Biom*) as the dependent variable and fragment size (F) as a continuous variable and resource type (R) and season (S) as factors with two levels each. The model was analyzed with an analysis of covariance (ANCOVA). ANCOVA is used for analysis of variance (ANOVA) designs in which an additional continuous variable is measured for each replicate. The covariate also contributes to variation in the response variable (Gotelli and Ellison 2004). To obtain the optimal model, Akaike information criteria (AIC) was used. AIC is useful because it gives the most parsimonious parameters when two models are compared. The best supported model has the lowest AIC compared with the other model(s) (Crawley 2004). Statistical analyses were carried out using R 2.9.0 software (R development Core Team 2006) and Statistica 7.0.

Results

A total of 658 specimens were recorded during the two seasons for both types of dung in all fragments. Nineteen species from nine genera were captured in monkey dung during both seasons. Of the 19 species, 12 were tunnelers, 4 were rollers, and three dwellers. In contrast, only seven species from five genera were captured in cow dung: five were tunnelers, one was a dweller, and one a roller (Table 1; Fig. 2). The most abundant species in monkey dung during the dry season were the dweller *Eurysternus mexicanus* (Harold 1869) (199 individuals) and two tunneler species *Copris laeviceps* (Harold 1869) (64) and *Onthophagus batesi* (Howden and Cartwright 1963) (29). In cow dung during the dry season, only tunneler species were captured (Table 1): *C. laeviceps* (33), *Ateuchus illaesum* (Harold 1868) (6), and *O. batesi* (4). During the rainy season, 157 individuals were captured in monkey dung. The most abundant species for this type

Table 1. Dung beetle guild abundance and richness in all fragments by season and resource type

	Guild	Area covered in dry season (ha)						Area covered in rainy season (ha)						Total
		3	10.3	40.5	112	265.5	700	3	10.3	40.5	112	265.5	700	
Monkey dung														
Ateuchus illaesum	T					14	2	1	3	1	2	6	2	31
Canthidium centrale	T						1							1
Canthon cyanellus	R	7		1	3					1			2	14
C. euryscelis	R				1									1
C. femoralis	R				8	1								9
C. subhyalinus	R					3								3
C. vasquezae	R	14												14
Copris laeviceps	T	5	5	1	31	10	12	5	6	16	12	10	27	140
C. lugubris	T			2				1		6				9
Deltochilum gibbosum	R												1	1
D. pseudoparile	R	1			1									2
D. satanas	T												1	1
Eurysternus caribaeus	D	1			2						1	1		5
E. foedus	D	15	1		2		1	3	1	1				24
E. mexicanus	D	83	32		15	67	2			9		3		211
Onthophagus batesi	T	21			7		1	20	1		6	1	3	60
O. landolti	T									3				3
O. rhinolophus	T			12	5	6								23
Phanaeus endymion	T			1				1						2
Total		147	38	17	75	101	19	31	11	37	21	21	36	554
No. spp.		8	3	5	10	6	6	7	5	7	5	7	6	
Cow dung														
Ateuchus illaesum	T	1		1		2		2	1		3	4	2	16
C. femoralis	R									1				1
C. laeviceps	T		4	7	4		18		8	7	10	7	4	69
D. satanas	T							1						1
E. mexicanus	D							3	1	1	1	5		11
Onthophagus batesi	T	4												4
O. landolti	T	2												2
Total		7	4	8	4	2	18	6	10	9	14	16	6	104
No. spp.		3	1	2	1	1	1	3	3	3	3	3	2	

D, dweller; R, roller; T, tunneler.

of dung were *C. laeviceps* (76 individuals), *O. batesi* (31), and *A. illaesum* (15). In cow dung, 61 individuals were captured; the most abundant species were *C. laeviceps* (36), *A. illaesum* (12), and *E. mexicanus* (11).

Dung Removal Rates. The mixed effects model found no effect of the following fixed effects on dung removal rates: fragment size ($P = 0.41$), the fragment size × resource type interaction ($P = 0.50$), and the fragment size × season interaction ($P = 0.23$). In contrast, resource type ($P \leq 0.01$), season ($P \leq 0.01$), and the resource type × season interaction ($P = 0.01$) had significant effects on dung removal rates (Table 2). In general, removal rates were greater for monkey dung than for cow dung, and the difference was greater during the dry season. Cow dung removal rates were higher in the rainy season than in the dry season for most of the fragments, except for the 700-ha fragment, where the pattern of dung removal was similar for the dry and rainy seasons (Fig. 3). In the lme, the random effects model reflected an effect of time on

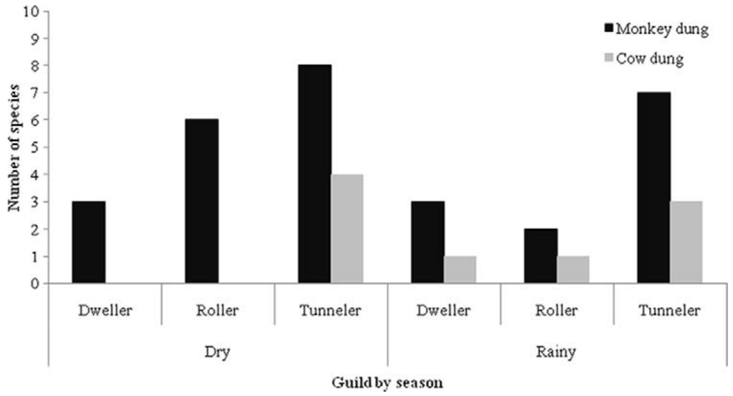

Fig. 2. Differences in species richness by guild (dwellers, rollers, and tunnelers) for monkey and cow dung in all fragments during the dry and rainy seasons.

Table 2. LME with repeated measures in time (*H*)

	Estimated reg coefficient	SE	df	*t*-value	*P* value
Random effects: (time [*H*] over traps nested within fragments)					
Intercept	4.430	4.620	215	0.95	0.338
H	1.407	0.087	215	16.03	0.000
	SD	Corr			
Intercept	44.524	(Intr)			
H	1.110	−0.92			
Residual	22.178				
Fixed effects: Rem as a function of $F \times R \times S$					
Intercept	31.683	8.742	216	3.624	0.00
F	−0.023	0.028	64	−0.825	0.41
S	36.022	12.363	64	2.913	<0.01
R	54.252	12.363	64	4.388	<0.01
$S \times R$	−45.512	17.484	64	−2.603	0.01
$F \times R$	−0.026	0.039	64	−0.670	0.50
$F \times S$	−0.047	0.039	64	−1.195	0.23
$S \times R \times F$	0.119	0.056	64	2.123	0.03

For the random effects of time (*H*) and the fixed effects of fragment size (*F*), season (*S*), and resource type (*R*) on dung removal rates.

dung removal ($P \leq 0.01$). There was a negative correlation between the amount of dung and time, indicating that the rate of dung removal was high at the beginning but decreased over time. In all fragments, the rate of dung removal was high from 24 to 48 h, after which the consumption of dung slowed (Table 2; Fig. 3a–d).

Effect of Fragment Size, Resource Type, and Season on Dung Beetle Biomass. The ANCOVA showed that fragment size ($P = 0.397$), season ($P = 0.924$), and the fragment size × season interaction ($P = 0.501$) had no effect on dung beetle biomass. In contrast, resource type had a significant effect on dung beetle biomass ($P \leq 0.001$), with monkey dung attracting more dung

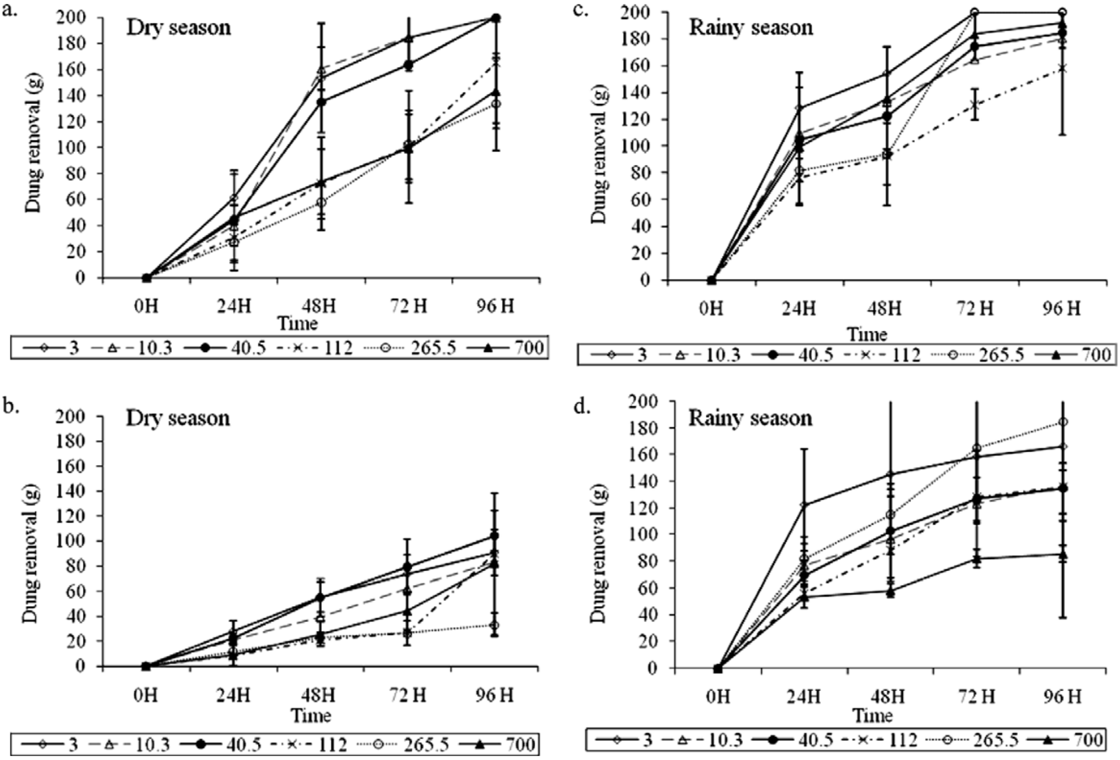

Fig. 3. Dung removal rates per fragment from 24 to 96 h of resource availability in the dry season for (a) monkey and (b) cow dung and in the rainy season for (c) monkey and (d) cow dung.

Table 3. Total dung beetle biomass (g) by fragment, season, and resource type

Fragment size (ha)	Dry season		Rainy season	
	Monkey dung (g)	Cow dung (g)	Monkey dung (g)	Cow dung (g)
3.0	4.98	0.16	0.16	0.36
10.3	1.27	0.28	0.28	0.17
40.5	4.12	0.88	1.65	0.15
112	3.65	0.28	0.55	0.39
265.5	2.58	0.03	0.78	0.50
700	1.06	1.26	1.08	0.12

beetle biomass than cow dung. Monkey dung attracted 81.3% of the total dung beetle biomass in all fragments over the course of this study. The interaction between fragment size and resource type also had an effect on dung beetle biomass ($P = 0.02$). A higher biomass was captured for monkey dung (12.46 g) in fragments with an area of <100 ha than in fragments >100 ha (7.29 g). In contrast, for cow dung, beetle biomass in all fragments was especially low with respect to monkey dung (4.58 g; Tables 3 and 4). The season × resource type interaction ($P \leq 0.01$) also had a significant effect on biomass. Dung beetle biomass was greater during the dry season (17.66 g) than during the rainy season (4.05 g) for monkey dung, but for cow dung, the seasonal differences were not pronounced (2.89 g in the dry season and 2.14 g in rainy season; Fig. 4).

Discussion

Several studies have shown that coprophagous dung beetles exhibit some degree of specificity for different types of mammalian dung (Matthews 1972, Hanski and Cambefort 1991, Hill 1996, Estrada et al. 1999, Vernes et al. 2005, Larsen et al. 2006, Rahagalala et al. 2009). Halffter and Matthews (1966) proposed that Neotropical dung beetles coevolved with mammal herbivores, a relationship that explains their preference for native dung and lack of preference for exotic cow and horse dung; animals that were introduced in the Neotropics only 500 yr ago (Vieira et al. 2008). Rahagalala et al. (2009) also proposed that dung beetles had coevolved with a diverse group of primates in Madagascar, and although cattle were introduced there 1,000 yr ago, as a new type of resource, cattle dung is only attractive to few dung beetle species and the great majority of them maintain their ancestral food preferences. In our study, dung beetles preferred monkey dung to cow dung, suggesting that, in Los Tuxtlas, most dung beetle species are adapted to native mammalian herbivore dung and maintain their food preferences, even when exotic new resources are available.

Table 4. Analysis of covariance for the effects of fragment size (*F*), season (*S*), and food resource (*R*) on dung beetle biomass

	Estimate SE	*t*-value	*P*	
Intercept	0.085	0.138	0.615	0.54
F	0.000	0.000	0.870	0.39
S	0.018	0.195	0.096	0.92
R	1.120	0.195	5.727	<0.01
$F \times S$	−0.000	0.000	−0.688	0.50
$F \times R$	−0.001	0.000	−2.519	0.02
$S \times R$	−0.861	0.276	−3.114	<0.01

The triple interaction $F \times S \times R$ was removed from the initial model after applying the AIC criteria.

Residual SE: 0.268 on 16 df, multiple R^2: 0.752, adjusted R^2: 0.644, *F*-statistic: 6.952 on 7 and 16 df, $P < 0.001$.

The use of native or exotic dung as bait in our study resulted in large differences in estimates of dung removal rates by dung beetles under identical ecological conditions. Dung beetle activity is expected to be higher during the rainy season (Gill 1991), and consequently, dung removal rates are expected to increase during the rainy season relative to the dry season. Dung removal rates decrease during the dry season, among other causes, because low soil moisture and increased soil hardness can affect burying behavior (Nyeko 2009). In our study, we found higher removal rates for monkey dung than for cow dung, and the difference was more evident during the dry season. Furthermore, the removal rate of monkey dung was similar during both seasons, whereas for cow dung, the removal rate was higher during the rainy season; hence, the conclusion one draws on the patterns of dung removal depends on the type of dung being used.

Dung beetle species richness, abundance, and biomass in tropical forests are thought to decrease during the dry season and increase during the rainy season (Gill 1991), which is the reproductive period for dung beetles (Halffter and Matthews 1966, Vernes et al. 2005, Andresen 2008). Dung beetle species richness, abundance, and biomass were greater in monkey dung as a native resource than in the exotic cow dung. In addition, dung beetle species richness, abundance, and biomass were higher during the dry season than during the rainy season for monkey dung but not for cow dung, confirming that there are marked differences in dung beetle abundance and species richness when different resources are used. In a mosaic of vegetation ranging from open scrub to forest that covers part of the Brazilian coastline, Vieira et al. (2008) found that a high variation in species richness and abundance of dung beetles is an effect of the type of bait—in their case, cattle and human dung (considered an excellent bait for attracting dung beetles; see Larsen et al. 2006). A high abundance of dung beetles was found in monkey dung during the dry season in some of our fragments (such as the 3- and 115-ha fragments). These fragments might be retaining and/or attracting more dung beetles during this period because of the presence of monkey troops or other mammals that result in a high availability of food in these fragments (Andresen 2003). The relationship between mammal diversity in each fragment and the abundance of dung beetles in such fragments must be taken into account in future studies.

The biomass and body size of dung beetles are ecologically relevant characteristics, because large-sized species with high biomass such as *Dichotomius* and *Phanaeus* remove and bury large amounts of ex-

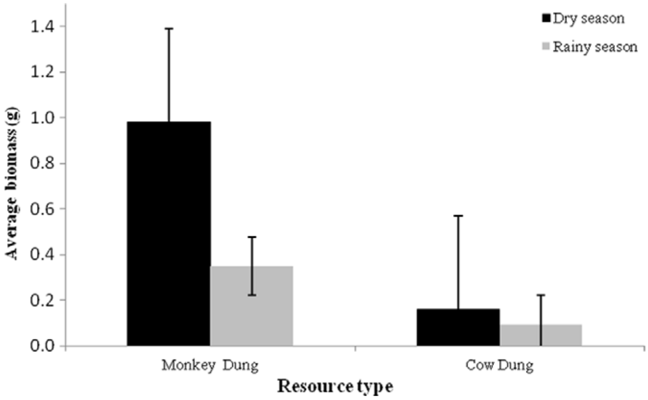

Fig. 4. Dung beetle biomass as a function of season and resource type (M, monkey dung; C, cow dung). Bars indicate SE.

crement faster than smaller species do (Andresen 2003, Anduaga 2004). The majority of species with largest accumulated biomass collected in our study belonged to the tunneler guild, considered the most important guild in the dung removal and seed incorporation into the soil (Andresen 2003). The most abundant species was *E. mexicanus,* a dweller species that occurs occasionally in forests, and *C. laeviceps,* a forest tunneler (Favila and Díaz 1997, Favila 2005), which was present in all fragments on both types of food. *Copris laeviceps* could be the most important species for dung removal in Los Tuxtlas,and accounted for the greatest biomass accumulation during both seasons. In contrast small biomass of roller species, such as *C. euryscelis* Bates, 1887, *C. femoralis, C. subhyalinus* Harold, and *C. vasquezae* Martinez, Halffter and Halffter, were found only in native dung, confirming that this guild is more selective (Slade et al. 2007) and maintains preference for native dung, even when cow dung is offered as an alternative food resource. Rosenlew and Roslin (2008) concluded that, whereas fragmentation can affect the composition of dung beetle assemblages, this was not reflected in ecosystem function because the loss of biomass for average species in forests is compensated by a direct increase in the biomass of other species. In our study, an increase in medium and small beetle biomass forest species, such as *Copris* and *Onthophagus* species (respectively), could compensate for the loss of large tunneler species such as *Dichotomius* and *Phanaeus* in fragments.

Dung beetle biomass was affected by the relationships between fragment size, resource type, and season. However, dung removal rates were only affected by resource type and season. Why is dung beetle biomass affected by forest fragmentation, but not the processes of dung removal? Klein (1989) proposed that forest fragmentation reduces abundance and species richness in fragments <1 ha and those that had been isolated for 1–5 yr compared with continuous forests in Central Amazonia. However, studies performed after Klein's work in the same area several years later (Andresen 2003, Quintero and Roslin 2005) showed that the abundance and species richness in these fragments tended to recover, with the rate of recovery depending on each species. In Los Tuxtlas, forest fragmentation began almost 40 yr ago, and therefore species and individuals may not be suffering at this time the same fluctuations in space and time that occurred when fragmentation began. Halffter and Arellano (2002) suggested that, when the availability of food increases in large forest fragments, there is an increase in abundance that produces an increase in biomass, but not necessarily a modification in the community; the opposite occurs when there is a reduction in tree cover. Although in Los Tuxtlas dung beetle community structure and dung beetle biomass were affected by fragmentation, the fact that the rate of dung removal was similar in the different fragments suggests that a few, abundant species are responsible of the incorporation of dung into the soil.

Habitat loss and the concomitant decrease in native food resource availability for dung beetle species is a challenge at the conservation level (Nichols et al. 2007, Nichols et al. 2008). Reducing logging, changes in soil use, and in particular the loss of large native mammal species would result in maintaining a relatively stable and healthy dung beetle community. In turn, dung beetle conservation will result in ecosystem services such as soil aeration and nutrient cycling and will also prevent such ecological problems as the accumulation of dung and dead organic matter, loss of soil nutrients, contamination, and decreased seed germination (Andresen 2003, Nichols et al. 2009). This study showed that dung removal rate has to be analyzed using native dung as food resource. Using resources (i.e., cow and other livestock dung) in tropical forest fragments where these resources do not have a long history of use by dung beetle species may bias our understanding of the patterns of dung removal rates, guild composition, biomass, species richness, and seasonality. The analysis of dung removal rates as part of the nutrient cycling process is a valuable tool for evaluating the correct functioning of the ecosystem. It also highlights the importance of preserving not only dung beetle communities, but native mammals in fragmented landscapes to preserve the biodiversity and ecosystem processes.

Acknowledgments

ScarabNet is an international group of dung beetle taxonomists, ecologists, and systematists dedicated to developing the information infrastructure needed to establish Scarabaeinae dung beetles as a functioning invertebrate focal taxon for the study of biodiversity and conservation. We thank the Estación de Biología Tropical de la UNAM in Los Tuxtlas, Veracruz, and especially R. Coates for permission to use the Station laboratories; R. Guevara for help with statistical analysis; F. Horgan and J. Rull for valuable comments to the manuscript and the English revision; our field guides E., E., and D. Domingo, who helped us with field work; the Banderilla Zoo in Xalapa and the personnel of the Universidad Veracruzana Flora and Fauna Park in Pipiapan, especially D. Antonio, for providing us the monkey dung; and the owners of fragments close to the Biological Station for permission to work on their land. B. Delfosse revised the English. We gratefully acknowledge contributions of anonymous referees and D. Horton, who provided suggestions for improvement of the manuscript. S.A. was a CONACyT doctoral fellow (213549) for the duration of this study.

References Cited

Aguirre, A., and R. Dirzo. 2008. Effects of fragmentation on pollinator abundance and fruit set of an abundant understory palm in a Mexican tropical forest. Biol. Conserv. 141: 375–384.

Andresen, E. 1999. Seed dispersal by monkeys and the fate of dispersed seeds in the Peruvian rainforest. Biotropica 31: 145–158.

Andresen, E. 2003. Effect of forest fragmentation on dung beetle communities and functional consequences for plant regeneration. Ecography 26: 87–97.

Andresen, E. 2008. Short-term temporal variability in the abundance of tropical dung beetles. Insect Conserv. Divers. 1: 120–124.

Anduaga, S. 2004. Impact of the activity of dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae) inhabiting pasture land in Durango, Mexico. Environ. Entomol. 33: 1307–1312.

Beck, H., and J. Terborgh. 2002. Groves versus isolates: how spatial aggregation of *Astrocaryum murumuru* palms affects seed removal. J. Trop. Ecol. 18: 275–288.

Carlo, T. A., and J. M. Morales. 2008. Inequalities in fruit-removal and seed dispersal: consequences of bird behavior, neighborhood density and landscape aggregation. J. Ecol. 96: 609–618.

Cramer, J. M., R.C.G. Mesquita, T. Vizcarra Bentos, B. Moser, and G. B. Williamson. 2007. Forest fragmentation reduces seed dispersal of *Duckeodendron cestroides,* a central Amazon endemic. Biotropica 39: 709–718.

Crawley, M. J. 2004. Statistical computing. An introduction to data analysis using S-Plus. J. Wiley & Sons, Chichester, West Sussex, England.

Dirzo, R., and A. Miranda. 1991. El límite boreal de la selva tropical húmeda en el continente americano: contracción de la vegetación y solución de una controversia. Interciencia 16: 240–247.

Dirzo, R., and M. C. Garcia. 1992. Rates of deforestation in Los Tuxtlas, a Neotropical area in southeast Mexico. Conserv. Biol. 6: 84–90.

Estrada, A., A. Anzures Dadda, and R. Coates-Estrada. 1999. Tropical rain forest fragmentation, howler monkeys (*Alouatta palliata*) and dung beetles at Los Tuxtlas, Mexico. Am. J. Primates 48: 253–262.

Everitt, B. 2005. Analysis of repeated measures data, pp. 171–199. *In* An R and S-Plus companion to multivariate analysis. Springer, London, United Kingdom.

Favila, M. E. 2005. Los escarabajos y la fragmentación, pp. 135–157. *In* S. Guevara, J. Laborde, and G. Sánchez-Ríos (eds.), Los Tuxtlas: El Paisaje de la Sierra. UNION EUROPEA, Instituto de Ecología, Mexico D.F., Mexico.

Favila, M. E., and A. Díaz. 1997. Escarabajos coprófagos y necrófagos, pp. 383–384. *In* S. González, R. Dirzo, and R. C. Vogt (eds.), Historia Natural de los Tuxtlas. UNAM, Instituto de Ecología, A.C., Mexico D.F., Mexico.

Favila, M. E., and G. Halffter. 1997. The use of indicator groups for measuring biodiversity as related to community structure and function. Act. Zool. Mex. 72: 1–25.

Forget, P. M. 1996. Removal of seeds of *Carapa procera* (Meliaceae) by rodents and their fate in rainforest in French Guiana. J. Trop. Ecol. 12: 751–761.

Freymann, B., R. Buitenwerf, O. DeSouza, and H. Olff. 2008. The importance of termites (Isoptera) for the recycling of herbivore dung in tropical ecosystems: a review. Eur. J. Entomol. 105: 165–173.

Gardner, T., M.I.M. Hernandez, J. Barlow, and C. A. Peres. 2008. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests in neotropical dung beetles. J. Appl. Ecol. 45: 883–893.

Gill, B. D. 1991. Dung beetles in tropical American forest, pp. 211–229. *In* I. Hanski and Y. Cambefort (eds.), Dung beetle ecology. Princeton University Press, Princeton, NJ.

Gotelli, N. J., and A. M. Ellison. 2004. A primer of ecological statistics. Sinauer, Sunderland, MA.

Halffter, G., and E. G. Matthews. 1966. The natural history of dung beetles of the subfamily Scarabaeinae. Fol. Entom. Mex. 12-. 14: 1–312.

Halffter, G., and L. Arellano. 2002. Response of dung beetle diversity to human-induced changes in a tropical landscape. Biotropica 34: 144–154.

Hanski, I., and Y. Cambefort. 1991. Dung beetle ecology. Princeton University Press, Princeton, NJ.

Hill, C. J. 1996. Habitat specificity and food preferences of an assemblage of tropical Australian dung beetles. J. Trop. Ecol. 12: 449–460.

Horgan, F. G. 2002. Shady field boundaries and the colonization of dung by coprophagous beetles in Central American pastures. Agric. Ecos. Environ. 92: 25–39.

Horgan, F. G. 2005. Aggregated distribution of resources creates competition refuges for rainforest dung beetles. Ecography 28: 603–618.

Horgan, F. G. 2008. Dung beetle assemblages in forests and pastures of El Salvador: a functional comparison. Biodivers. Conserv. 17: 2961–2978.

Howden, H. F., and V. G. Nealis. 1975. Effects of clearing in a tropical rain forest on the composition of the coprophagous scarab beetle fauna (Coleoptera). Biotropica 7: 77–83.

Hughes, L., and M. Westoby. 1990. Removal rates of seeds adapted for dispersal by ants. Ecology 71: 138–148.

Klein, B. C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. Ecology 70: 1715–1725.

Laurance, W. F., H. L. Vasconcelos, and T. E. Lovejoy. 2000. Forest loss and fragmentation in the Amazon: implications for wildlife conservation. Oryx 34: 39–45.

Larsen, T. H., and A. Forsyth. 2005. Trap spacing and transect design for dung beetle biodiversity studies. Biotropica 37: 322–325.

Larsen, T. H., A. Lopera, and A. Forsyth. 2006. Extreme trophic and habitat specialization by Peruvian dung beetles. Coleop. Bull. 60: 315–324.

Matthews, E. G. 1972. A revision of the Scarabaeinae dung beetles of Australia I. Tribe Onthophagini. Aus. J. Zool. 9(Suppl): 3–330.

Medellin, R., and O. Gaona. 1999. Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. Biotropica 31: 478–485.

Mendoza, E., R. Dirzo, and J. Fay. 2005. A quantitative analysis of forest fragmentation in Los Tuxtlas, southeast Mexico: patterns and implications for conservation. Rev. Chil. Hist. Nat. 78: 451–467.

Nichols, E., T. Larsen, S. Spector, A. Davis, F. Escobar, M. Favila, K. Vulinec, and the Scarabnet Research Network. 2007. Global dung beetle response to tropical forest modification and fragmentation: a quantitative literature review and meta-analysis. Biol. Conserv. 137: 1–19.

Nichols, E., S. Spector, J. Louzada, T. Larsen, S. Amezquita, M. Favila, and the T.S.R. Network. 2008. Ecological functions and ecosystem services of Scarabaeinae dung beetles: a review. Biol. Conserv. 141: 1461–1474.

Nichols, E., T. A. Gardner, C.A. Peres, S. Spector, and the Scarabaeinae Research Network. 2009. Co-declining mammals and dung beetles: an impending ecological cascade. Oikos 118: 481–487.

Nyeko, P. 2009. Dung beetle assemblages and seasonality in primary forest and forest fragments on agricultural landscapes in Budongo, Uganda. Biotropica 41: 476–484.

Quintero, I., and T. Roslin. 2005. Rapid recovery of dung beetle communities following habitat fragmentation in central Amazonia. Ecology 86: 3303–3311.

Rahagalala, P., H. Viljanen, J. Hottola, and I. Hanski. 2009. Assemblages of dung beetles using cattle dung in Madagascar. Afr. Entomol. 17: 71–89.

Rosenlew, H., and T. Roslin. 2008. Habitat fragmentation and the functional efficiency of temperate dung beetles. Oikos 117: 1659–1666.

Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation. Conserv. Biol. 5: 18–32.

Slade, E. M., D. J. Mann, J. F. Villanueva, and O. T. Lewis. 2007. Experimental evidence for the effects of dung beetle functional group richness and composition on ecosystem function in a tropical forest. J. Anim. Ecol. 76: 1094–1104.

Soto, M. 2004. El Clima, pp. 195–198. *In* S. Guevara, J. Laborde, and G. Sánchez-Ríos (eds.), Los Tuxtlas: El paisaje de la sierra. Instituto de Ecología, Xalapa, Mexico.

Spector, S. 2006. Scarabaeinae dung beetles (Coleoptera: Scarabaeidae: Scarabaeinae): an invertebrate focal taxon for biodiversity research and conservation. Coleopterist Bull. 5: 71–83.

Vander Wall, S. B., K. M. Kuhn, and M. J. Beck. 2005. Seed removal, seed predation, and secondary dispersal. Ecology 86: 801–806.

Vernes, K., L. C. Pope, C. J. Hill, and F. Bärlocher. 2005. Seasonality, dung specificity and competition in dung beetle assemblages in the Australian wet tropics, northeastern Aust. J. Trop. Ecol. 21: 1–8.

Vieira, L., J. Louzada, and S. Spector. 2008. Effects of degradation and replacement of southern Brazilian coastal sandy vegetation on the dung beetles (Coleoptera: Scarabaeidae). Biotropica 40: 719–727.

Vulinec. K. 2002. Dung beetle communities and seed dispersal in primary forest and disturbed land in Amazonia. Biotropica 34: 297–309.

Weeny, D. G. 2000. Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. Ecol. Monogr. 70: 331–351.

Wilcox, B. A., and D.D.F. Murphy. 1985. Conservation strategy: the effects of fragmentation on extinction. Am. Nat. 125: 879.

Received 6 July 2009; accepted 22 September 2009.