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Seasonal change in abundance of large nocturnal dung beetles (Scarabaeidae) in a Costa Rican deciduous forest and adjacent horse pasture

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The five species of adult nocturnal dung beetles (Scarabaeinae, Scarabaeidae) that degrade most horse dung during the rainy season in Santa Rosa National Park, Costa Rica, were censused with horse dung-baited traps from shortly before the rainy season began until the end of the rainy season in a tropical deciduous forest and nearby pasture. *Dichotomius yucatanus* and *D. carolinus,* small and large species respectively, had their peak abundance during the first half of the rainy season, while *D. centrale,* intermediate in size, had its peak adult abundance in the second half of the rainy season. Adults of *Copris lugubris,* also intermediate in size, occurred at low density throughout the rainy season. All but the rarest beetle species (*Deltochilum lobipes*) were more abundant in the forest than in the pasture, with *Dichotomius centrale* showing this habitat segregation most strongly. Homogenizing the dung among the traps reduced the among-trap within-site variation in numbers of beetles caught. The present dung beetle fauna is probably only a remnant of what was supported by the Pleistocene megafauna. The patterns of horse and cow dung use by the contemporary dung beetle fauna may well be nothing more than an ecological response over the past 300 yr by species sufficiently flexible to have survived since the Pleistocene on the dung rain generated by a native tropical fauna poor in large mammals.

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Пять видов взрослых навозных жуков *Scarabaeinae Scarabaeidae* с ночной активностью, которые разрушают большую часть конского навоза в сезон дождей в Национальном Парке Санта Роза (Коста Рика) переписаны с помощью ловушек с конским навозом перед началом периода дождей и до его конца в тропическом листопадном лесу и около пастбища. *Dichotomius yucatanus* и *Dichotomius carolinus* - мелкий и крупный виды, имеют максимум обилия в первой половине сезона дождей, а *D. centrale* - средних размеров, имеет максимум обилия имаго во второй половине сезона дождей. Имаго *Copris lugubris*, также средних размеров, встречаются в небольшом количестве в течение всего дождевого сезона. Все, кроме очень редкого вида жука *Deltochilum lobipes* более многочисленны в лесу, нежели нв пастбище, а *Dichotomius centrale* сегрегируется в этом биотопе более строго. Гомогенизация навоза между ловушками снижает вариящии в количестве пойманных жуков в разных ловушках в пределах одного биотопа. Настоящая фауна навозных жуков по-видимому лишь остаток той фауны, которая поддерживалась плейстоценовой мегафауной. Конский и коровий навоз используются современной фауной навозных жуков и это может рассматриваться как экологическая реакция последних 300 лет у видов, достаточно пластичных и сохранившихся с плейстоценового времени на потоке навоза от нативной тропической фауны, бедной крупными млекопитающими.

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Introduction

Conspicuous seasonality of numbers and species of insects in tropical habitats is well-documented (e.g., Gillon 1971, Janzen 1973, Wolda 1978a, 1978b, Wolda and Fisk 1981, Owen 1971). Seasonal fluctuation in food availability is recognized as a common correlate of tropical insect seasonality but difficult to tease out of the morass of other environmental parameters that change with the alternation of the wet and dry seasons. The dung of large mammals, food for a wide variety of insects, is a food type that fluctuates relatively little in amount as compared with foods such as foliage of deciduous trees, fruits and seeds, flower nectar, pollen, etc. Because of this, insects that use dung might be expected to show substantially less seasonal fluctuation in numbers than do those that use other food types in the same habitat. More specifically, there seems to be a general feeling among collectors of Neotropical dung beetles (Scarabaeidae: Scarabaeinae) that while numbers may fluctuate somewhat, most species of dung beetles can be captured at most times of the year if the right baits are used. While this impression is probably close to reality in lowland moist or wet forest sites, here I document the opposite impression: in lowland Central American habitats with a six month rain-free dry season, the dung-degrading activity of the major dung-degrading beetles is extremely seasonal, just as is the case with dung beetles in East African elephant dung (Anderson and Coe 1974).

In the lowland deciduous forest and pasture habitats of northwestern Costa Rica, horse and cattle dung accumulates in a relatively intact state throughout the six month dry season (December-May). During the rainy season, it disappears within a few days. This seasonal variation in dung decomposition is due largely to variation in numbers of large nocturnal dung beetles that arrive at the dung pile. During the first half of the rainy season, these beetles bury or churn at least half, and usually all, of the dung into the soil within several days of its deposition (as is the case in other tropical areas – e.g., Bornemissza 1960, Bornemissza and Williams 1970, Gillard 1967, Heinrich and Bartholomew 1979, Anderson and Coe 1974). The number of large nocturnal dung beetles that arrive at a dung pile varies conspicuously among habitats as well. While dung beetles and other dung-using insects are known to vary in abundance in dung with season and habitat (e.g., Mohr 1943, Halffter and Matthews 1966, Edmonds and Halffter 1972, Anderson and Coe 1974, Macqueen and Beirne 1975, Howden and Nealis 1975, 1978, Merritt and Anderson 1977, Koskela and Hanski 1977, Coe 1977, Bartholomew and Heinrich 1978, Heinrich and Bartholomew 1979, Hanski and Koskela 1979, Hanski 1980a, b, c, Howden and Young 1981), there are no neotropical studies documenting the details of seasonal change in numbers of adult beetles in general, and large nocturnal dung beetles in particular.

For several reasons I focus on the five largest species to arrive at horse dung at night in Santa Rosa National Park. First, they degrade nearly all the dung of horses and cattle during the rainy season in the Park and its adjacent cattle ranches, in a habitat representative of that which occupies most of the coastal Pacific lowlands of Central America. Second, they are large enough to census easily and accurately. Third, they are large enough to be potential buriers of the seeds that often occur in horse dung. This may result in escape of the seeds from those species of small rodents that forage in dung for seeds (Janzen 1982b, c). Fourth, while the interaction of horse dung, seeds, dung beetles and small rodents might appear to be of little interest because the horse is introduced, in fact the introduced horse is a gift from the Pleistocene and our only chance to examine how the Pleistocene megafauna may have interacted with its vegetation in Central America (Janzen 1981a, b, 1982a, Janzen and Martin 1982). The study was conducted in a lightly and heterogeneously grazed mix of forest and grassland, and the seasonal fluctuations in dung beetle density described are quite likely to be representative of those that occurred 10000 years ago in Central American lowland strongly seasonal habitats.

Materials and methods

Study site. The forest and pasture dung beetle trapping sites lie within 1 km of the main administration area of park headquarters, Santa Rosa National Park, NW Guanacaste Province, Costa Rica (10800 ha, elevation 300 m, 10°45′ to 11°00′N). The two pasture trapping sites (AP and BP) are at the south end of the south horse pasture, which is immediately to the west of the administration area. This pasture, about 10 ha in extent, was cut out of deciduous forest at least 100 yr ago and is part of the pasture and forest mosaic that covers the central uplands of the park. The pasture is bounded by strips of 15–80 yr old regenerating forest, which are in turn bounded by other large abandoned pastures. It is largely grass and herb-covered, with scattered shrubs and small trees. During the 1980 rainy season, it contained 1–17 horses. The number of horses in the pasture fluctuated by the day and week; when it had few horses, it was usually because most had been moved to an adjacent pasture about 300 m from the sites of the dung beetle traps. The general appearance of the horse pasture is similar to the heavily used horse and cattle pastures in the vicinity of the park.

The two pasture trapping sites were 140 m apart and separated by about 3 m of elevation. Site AP was about 20 m from the edge of a 4–8 m tall forest, while site BP was about 50 m from forest of this height. Both trapping sites lacked overhanging trees or shrubs. Since winds frequently blow in different directions during the rainy season at Santa Rosa, one site cannot be viewed as downwind of the other at this time of year.

The two forest trapping sites (AF and BF) were in the 40–80 yr old regenerating forest along the north and east side of the park entrance road. They were 100 m (AF) and 400 m (BF) north of the four-way intersection of the road to the Casona and the road to Hacienda Rosa Maria and the road to the park administration area. This forest is locally known as "Hubbell's Woods" and is the gridded forest used by S. B. Hubbell for studies of leaf-cutter ants and forest succession. It is largely deciduous during the long dry season but contains a few species of evergreen trees and shrubs. It contains at least 200 species of perennial plants. It is bounded to the south by asphalt road, woody regeneration and abandoned broken pasture edge; in other directions it is contiguous with many square kilometers of deciduous forest and evergreen forest that contained old pastures which are now returning to woody vegetation.

The two forest sites were about 150 m apart. Site AF was in a slightly drier portion of the forest, a site where all trees are totally bare during much of the dry season. During the rainy season the canopy-level foliage is less dense and more irregular at site AF. If there were several consecutive days without rain, the soil and litter dried out much more noticeably at site AF than at site BF. Site BF was about 8 m lower in elevation than AF and the soil in the area were generally more moist year-round than at site AF. Even during a breezy and rain-free portion of the rainy season, the habitat at site BF remained humid, cool and shady.

Santa Rosa National Park experiences the long dry season characteristic of the Pacific coastal plain of Central America. The rainy season starts abruptly in the first or second week of May and ends during the last weeks of November or early December. The soil dries out gradually and the vegetation becomes progressively more bare as the dry season progresses. Dry season days are windy and the sky is often cloudless, though there may be an occasional period of cloudy weather and even an occasional sprinkle. Sometime between late June and early August there is usually a period of 1–4 wk of relatively rain-free weather (the little dry season or "veranillo"). At Santa Rosa the total rainfall during the rainy season is usually between 1500 and 2000 mm.

The park owned about 30 horses that were variably distributed between the pasture trapping area and another large pasture about 400–600 m to the south. These two pasture areas were about equidistant from the site of the forest trapping sites, and about 600 m from the edge of the forest where I trapped. The other sources of horse and cattle dung within the park were the occasional horse ridden by a park guard on patrol and a herd of about 12 feral cattle that lived 1–2 km southeast of the general study area. There were no active cattle or horse pastures on private ranches within 6 km along three primary compass directions from the general study area. However, Hacienda Rosa Maria, a large private cattle ranch supporting many hundreds of cattle and a few horses, lies 3 km to the southeast of both trapping sites.

The beetles. From late May to early July (first and second months of the rainy season) at Santa Rosa, a pile of horse dung defecated at mid-day attracts dung beetles (Scarabaeinae) within minutes after it falls. Very small dung beetles burrow in or below the dung, feed on it, and bury some in the soil below the pile. Occasionally one or more species of large metallic green or blue dung beetles (*Canthon indigaceus chevrolati, Phanaeus excelsus, P. wagneri, Sulcophaneus cupricollis, P. eximius*) arrive and either form balls of dung to be rolled off and buried elsewhere (*C. i. chevrolati*) or bury dung directly below the dung pile (the other four species) (see Halffter and Matthews 1966, Woodruff 1973, Halffter 1977). Flies and other arthropods arrive as well, including several bright metallic green 2 cm long staphylinid beetles (*Eulissus chalybaeus*) that prey on medium-sized to small dung beetles and other insects. In the forest, the same sequence occurs as in grassland, but the large metallic-colored dung beetles usually do not appear. As dusk approaches in both habitats, large numbers of large black dung beetles (Fig. 1, Tab. 1) fly to the dung pile a few minutes after it is too dark to see it clearly. The most common is *Dichotomius yucatanus*.

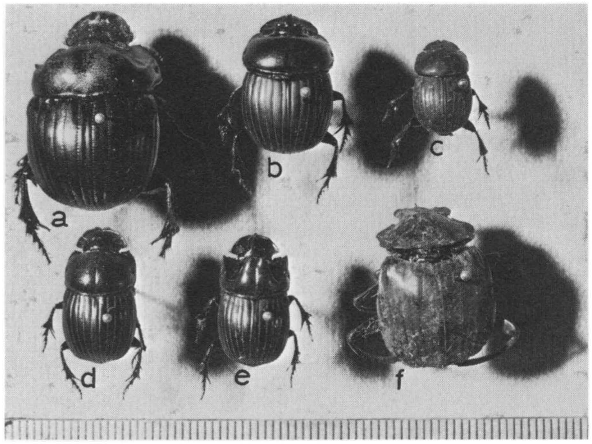

Fig. 1. The five large nocturnal dung beetles that arrive at horse dung in Santa Rosa National Park. a. *Dichotomius carolinus*. b. *D. centrale*. c. *D. yucatanus*. d. *Copris lugubris* female. e. *C. lugubris* male. f. *Deltochilum lobipes*.

Dichotomius centrale, D. carolinus and *Copris lugubris* arrive less frequently (Tab. 3). (*D. carolinus* has been identified as *Dichotomius colonicus* in other literature.) *Deltochilum lobipes* arrives only rarely. The first four of these species of nocturnal beetles mine through the dung and bury large amounts of it in vertical tunnels below the dung pile for feeding or oviposition (Matthews 1960, Halffter and Matthews 1966, Edmonds and Halffter 1972, Woodruff 1973). *D. lobipes* rolls very compact balls of dung away from the pile, or just feeds on the dung (Howden and Ritcher 1952, Woodruff 1973). By dawn, the dung pile is reduced to a flattened and finely mixed pile of dung and soil. The nocturnal dung beetles remain in the dung or in the tunnels below it until the following evening when most, if not all, leave in search of a new dung pile. The fresher a dung pile at sunset, the more beetles it attracts after dark. Further breakdown of the dung is done by other insects (including small dung beetles), rain erosion and microbial decomposition. A large adult dung beetle makes many tunnels in its lifetime, visits many dung piles, and may live as long as 1 to 2 months or more.

D. yucatanus and *D. carolinus* apparently have only one generation per year at Santa Rosa since teneral

Tab. 1. Body dimensions of the five large nocturnal Scarabaeinae dung beetles that come to horse dung in Santa Rosa National Park (n = 10).

Beetle	Live body weight (g) $\bar{X}$	s.d.	Length (mm)	Width (mm)
Dichotomius yucatanus	0.26	0.04	13–14	7–9
D. centrale	0.84	0.16	18–20	11–13
D. carolinus	2.19	0.42	25–32	17–19
Copris lugubris	0.50	0.08	16–19	9–10
Deltochilum lobipes	1.12	0.23	20–24	14–18

adults are encountered only at the beginning of the rainy season. Teneral adults of *D. centrale* are encountered frequently at the beginning of the second half of the rainy season, so there may be two generations per rainy season for this beetle at Santa Rosa. *C. lugubris* teneral adults are abundant only at the beginning of the rainy season and I suspect that at Santa Rosa this species is univoltine. This seasonality means that at Santa Rosa, the next generation of large dung beetles emerges from the soil many months after the parent lays the eggs. The five nocturnal species censused in this study all use cow as well as horse dung, and have been encountered in the forest burying coati dung (*Nasua nasua*) and human dung.

During extensive general collecting at horse dung during the past 3 yr at Santa Rosa, I have encountered only ten species of large scarabaeine dung beetles (including the diurnal species mentioned in an earlier paragraph). All have been collected in large numbers; if there are as yet uncollected species, they occur at extremely low density and/or in other Santa Rosa habitats. The large diurnal species arrive at horse dung only during daylight hours and occur at very low density compared to large nocturnal dung beetles. Therefore, they were not surveyed in this study. As the traps were set in late afternoon and generally checked in the first half of the morning, they were not used in a manner that would accurately census the diurnal species. Furthermore, some of the medium-sized diurnal species could fly out of the traps I used (see below). There is only one other large scarabaeine in the habitat: *Coprophanaeus telamon*. It is black, nocturnal, and weighs about 2 g, but has been caught only in traps baited with rotting meat (*Delochilum lobipes* is likewise attracted to rotting meat as well as to dung, e.g., Woodruff 1973). The small dung beetles (e.g., *Onthophagus*) were abundant in the traps but will require a different trapping method for accurate census. They are also of lesser interest because they process a minute volume of dung as compared to the array of large nocturnal dung beetles.

Traps. At each trapping site (AP, BP, AF, BF) four 27 cm × 27 cm cylindrical plastic buckets were buried with the rim level with the soil. The buckets were a meter apart and at the corners of a rough square. A disposable aluminium pie plate 22 cm in diameter was suspended by crossed wires over the mouth of the bucket and therefore at ground level. Small holes were punched in the pie plate to allow rainwater to flow through. The central position of the pie plate left a gap 2.5 cm wide between the rim of the pie plate and the lip of the bucket. Between one and 2.5 h before dark, a pile of 1–1.5 kg of horse dung was placed on the pie plate. This amount makes a domed pile about 8–10 cm deep. Beetles flying to the site either landed on the dung, or landed nearby and tried to walk to it. They either fell through the gap between the pie plate and the bucket rim at that time, or later fell into the bucket when attempting to move on, through or below the dung. In the bottom of each bucket a rock supported a screen about 5 cm above the bottom of the bucket. The original intent of the screen was to help the beetles stay out of rainwater accumulating in the bucket, but it also served in part to separate the beetles from the dung. The beetles often forced their way past the edges of the screen and thence to the bottom of the bucket, while much of the dung that they knocked into the bucket stayed above the screen.

The beetles were identified and counted in the field by either picking them individually out of the bucket and dung (in the bucket and on the pie plate), or by spreading handfuls of the dung and beetles on a tray and counting as the beetles were pushed or crawled from one end of the tray to the other. When the number of *Dichotomius yucatanus* per bucket was more than about 400, they were counted volumetrically with a 200-beetle measurer until most had been counted, and then the remainder were counted exactly. An experienced person can distinguish among the five species censused by rolling them between the fingertips. This is the case even when the hand and beetles are covered with dung. These beetles differ substantially in weight, linear dimensions, behavior and surface contour.

Survey records were kept individually for each trap but here have been pooled within a site, except where finer resolution seemed of interest (e.g., Tab. 3).

By observing the beetles at night and in the morning, it was determined that the five large nocturnal dung beetles could not fly out of the trap when the pie plate

Tab. 2. Number of dung beetles of five large nocturnal species trapped (and released) at four sites on 57 nights (four traps each night at each site) during the seven month rainy season (May-November) in a tropical deciduous forest.

Species	FOREST			PASTURE			Ratio of total numbers: forest/pasture
		Percent			Percent		
	Σ	Site AP	Site BP	Σ	Site AP	Site BP	
Dichotomius yucatanus	75017	40.5	59.5*	11287	51.0	49.0	6.6
D. centrale	1374	36.5	63.5*	179	58.7	41.3*	7.7
D. carolinus	819	41.3	58.7*	193	51.8	48.2	4.2
Copris lugubris	206	50.5	49.5	167	53.3	46.7	1.2
Deltochilum lobipes	4	25.0	75.0	9	44.4	55.6	0.4

*Between-site values are significantly different (ξ^2, $p < 0.05$).

Tab. 3. Numbers of large nocturnal dung beetles (Scarabaeidae) captured in four traps baited with horse dung at each of two forest sites and two grass pasture sites during the 1980 rainy season at Santa Rosa National Park, Guanacaste Province, Costa Rica.

Date		*Dichotomius yucatanus*		*D. carolinus*		Forest sites *D. centrale*		*Copris lugubris*		*Deltochilum lobipes*		*Dichotomius yucatanus*	
		Site A	Site B	Site A	Site B	Site A	Site B	Site A	Site B	Site A	Site B	Site A	Site B
May	1								1				
	2								1				
	3								2				
	7										1		
	9							2	7				
	11	39	11	5	8				1			5	5
	13	152	185	2	11	1						31	29
	15	398	55	6	4			12	2			12	47
	17	2001	686	25	29			1				144	132
	19	632	3981	1	9							299	115
	21	1330	1350	10	15	2	1					424	209
	23	995	2250	7	12	1	3		4			181	119
	25	1411	2742	23	8	10	5		2			25	284
	27	1317	1208	7	21	10	10		1			142	89
	29	908	1319	25	22	1	2	3	4			568	445
	31	2616	4374	29	41	2		4	2			1545	1510
Jun	2	1663	2133	30	52	1			1			12	57
	4	1384	1636	19	36	1	1	8	1			202	360
	6	1830	3241	27	26	2	3	11	1			353	441
	8	2358	2693	13	19	1	1	13	3			241	410
	10	12	862	2	10		2	3	4			25	200
	12	943	686	12	22	5		4				2	3
	14	428	735	3	26		1	3	10			307	111
	16	1469	2360	12	19	1	1	3	3		1	366	344
	18	987	1622	13	15			9	4			281	201
	20	913	791	13	15	1	2	4	3			139	93
	22	1477	2267	10	5		1	7	5			45	48
	24	1101	1221	7	10			3	6	1	1	64	57
	26	744	972		2	1		2	5			6	16
	28	482	444	3	2	1		2				21	10
	30	396	290	1	1							29	25
Jul	2	246	498		2		1	1	3			45	11
	4	195	607	1	3		1	1	3			23	14
	6	643	720		2	1	1	2	5			6	4
	8	302	721		3		1	3	2			14	3
	15	382	900		4		1		1			79	39
	25	409	868	14	10	4	5		1			66	42
Aug	1	158	164	3	4	3	8		2			17	16
	15	14	11			5	11	1				4	3
	22	6	12	1		6	5					12	24
	29	24	18	2		8	3					5	1
Sep	5	3	5	1	2	17	10		3			15	13
	15	1	4	2	7	27	52						1
	22	2	1	2		31	33					1	
	29		1			16	41						
Oct	6			2	1	36	50						
	13		1	2		61	62						
	20				2	57	60		1				
	27			3	1	43	72	1	1				
Nov	3					45	51		1				
	10					26	60	1	3				
	17					16	118		3				
	24					29	50						
Dec	1					12	26						
	8					6	62						
	15					11	43						
	22	1					13						

		Pasture sites					
D. carolinus		*D. centrale*		*Copris lugubris*		*Deltochilum lobipes*	
Site A	Site B	Site A	Site B	Site A	Site B	Site A	Site B
2	1			1			
2	2						
2				3			
16	11			1	1		
5	5				2		
11	12				1		
1	4			1	1		
6	5	1	2	2	6		
6	6	10	2	1	1		
7	15	2	4	3	2		
13	7	1	2	10	1	1	
3	1	1					
5	11	2	1	1	6		
5	5	3	2	1	5		
2	3	2	3	3	8		1
		7	1	7	6		
			1	2	5		
4				9	4		
	3	1		5	5		
4	1		3	3	13	1	
				8	2		
				4	1		
2				7	3		
				2			
				3			
					1		
				2	2		
		1		1			
1	1			1	1	1	
		1	2	1			
		2					
1			1	2			
		3	4				1
		2	1				
2		9	3	1			1
		1	4				
		3		1			
		4	3	2			
			1				
				1			
		3	1				
		3	2				
		9	4				
		5	1				
		10	3				
		5	7				
		5	6				
		5	7				2
		1	3				
		3			1		

was in place. Those that did fly upward hit the pie plate and fell back into the bucket. In preliminary experiments, marked beetles in the traps did not escape. However, most of the trapped beetles did not even try to fly out, but rather burrowed down through the mass of other beetles and dung. Many beetles also remained in the dung in the pie plate; it is the behavior of the three *Dichotomius* and *Copris lugubris* to remain in or below fresh dung not only through the night but through the following day as well. Since the traps were censused on the morning following baiting, they did not lose beetles by emigration from the dung on the pie plates.

Immediately after counting the beetles in the traps, the beetles were released. At the forest site, all dung was removed from the trapping area and spread on an asphalt highway 50 m away. Here it dried in the sun and was washed by rain. There was so little traffic that beetles left before they could be run over. By the following night it was no longer attractive to the five species of dung beetles that I censused. At the pasture sites, the dung was finely and widely scattered 50 or more meters away in the pasture. It was likewise not attractive to these five species of dung beetles by the next night. Trapping was not done on successive nights except during the first three nights when I was trying to determine if there were any beetles available before the rains started. By trapping every other night or at longer intervals, I allowed the captured dung beetles to redistribute themselves over the habitat during the intervening night(s).

All bait was horse dung that had been defecated between mid-morning and late afternoon (about 1000–1600 hours) by the horses in the horse pasture or the pasture immediately to the north of the horse pasture. None of the dung had been rained on before collection. Dung was placed in plastic bags or buckets at the time of collection. The containers were kept out of direct sun and the dung smelled fresh when placed out. Until the night of 16 June, each pie plate received dung from a different dung pile in the pasture. Therefore until 16 June, the age and origin of the bait in the different traps varied in a manner potentially of significance to the attractiveness of the dung. However, the dung was located haphazardly among the traps. Owing to the very large inter-trap variation within a site in numbers of beetles per trap, from 16 June onwards all dung collected was pooled in a large bucket and homogenized by mixing by hand. The same amount of dung was then placed on the pie plate as before 16 June, but it was a mix of dung from at least 3–6 horses and 0–4 h of age.

The amount of dung per pie plate was 1–1.5 kg because most horse dung piles in the pasture weighed 1–2 kg. The trapping scheme at any one site mimicked that of having four horses defecate at different times in the afternoon at one location. The forest site was as realistic as the grassland pasture site as a trapping location, since range horses often venture into forest to eat fruits and seek shade during mid-day high temperatures.

Results

Forest vs. pasture. A pile of horse dung in the Santa Rosa pasture was visited by many fewer large nocturnal dung beetles than was horse dung in nearby forest (Tab. 2). *Dichotomius yucatanus* and *D. centrale* were 6.6–7.7 times as abundant in the traps in the forest as in the pasture, and *D. carolinus* was 4.2 times as abundant in the traps in the forest as in the pasture. On the other hand, the two rarest species, *Copris lugubris* and *Deltochilum lobipes,* were about equally abundant in both habitats.

The two forest sites differed more between each other in beetle numbers per trap than did the two pasture sites (Tab. 2). For all three species of *Dichotomius,* the traps in the more moist forest site (site BF) caught significantly more beetles than did the traps in the drier site (site AF). In the pasture sites, such a between-site difference occurred only for *Dichotomius centrale.* This difference between forest and pasture was evident on a daily basis as well, but is not analysed in detail here. Suffice to note that on nights when very low catches occurred at the dry forest site (AF) there was often not a comparative decline in catches at the more moist forest site (BF) (eg., Tab. 3, 19, 23, 29 May). The large catches at the drier forest site were usually associated with generally rainy weather (heavy clouds, high humidity, prolonged light rain rather than short periods of intense thundershowers).

Seasonal changes. The arrival of adult large nocturnal dung beetles at piles of horse dung was not uniformly distributed through the year or within the rainy season (Tab. 3). In March 1980 and 1981 (middle of the dry season) there were no signs of any large nocturnal dung beetles at any horse dung in pasture or forest sites (observed during a different study of seeds in horse dung). In early May, 1980 before the first rain on the afternoon of 8 May, only one *Deltochilum lobipes* (a species that also uses carrion as food) and 13 *Copris lugubris* were taken at all sites on four nights of trapping. On the night of 9 May, two nights after the first rain (and 7 d before the next rain), no *Dichotomius* had yet appeared at the dung in the traps. Additionally, haphazard surveys of horse dung in and near the pasture site showed no sign of large nocturnal dung beetle foraging on the nights of 7–9 May. On the night of 10 May, specimens of *Dichotomius yucatanus* and *D. carolinus* were taken at blacklight-fluorescent light combinations in the vicinity of both the pasture and forest sites (*D. centrale* is almost never seen at lights no matter how abundant at dung). Beginning the night of 11 May, the numbers of *D. yucatanus* and *D. carolinus* increased rapidly to the highest levels in late May to the middle of June, and then declined gradually to September-early October. From 22 June to 12 July there was a period of sunny and breezy days with very little rain (veranillo); during this period there was a conspicuous dip in the numbers of *D. yucatanus* and *D. carolinus* in the traps (and at light and at other dung). Both the build-up and decline of these two beetles, and the slight depression of their density during the short mid-rainy season dry spell, was casually observed in 1979 at dung piles put out in forest and pasture for other purposes.

Dichothomius centrale behaved quite differently than did either *D. yucatanus* or *D. carolinus.* While *D. centrale* made its appearance in the traps first on 13 May in the forest and 25 May in the pasture, its density remained extremely low until early August when the numbers suddenly began to climb to a peak in late October and early November (Tab. 3). *D. centrale* became a rare beetle again in late December (about one month into the beginning of the dry season). While no further trapping was done after 22 December, I did observe that there was no sign of *D. centrale* at the naturally occurring dung in pasture or forest edge, or at my horse dung piles put out for other purposes on 30–31 December. Again, in March 1981, as in 1980, there were no signs of large nocturnal dung beetles at naturally occurring horse dung at Santa Rosa. The low density of *D. centrale* adults during the first half of the rainy season, followed by great increase in numbers in the second half of the rainy season, was casually observed in 1979 at dung piles put out in forest and pasture for other purposes.

Copris lugubris showed a seasonal presence much like that of *D. yucatanus* and *D. carolinus,* except that there was only a trivial increase in number at the time of peak density (June) as compared with the start of trapping, and that there were *C. lugubris* present from well before the first rains. However, the first *C. lugubris* caught were teneral and had presumably emerged from the soil only a few days before. *Deltochilum lobipes* was so rare in the traps that no statement can be made about seasonal changes in density. It was, however, present throughout the rainy season and before the first rain, and I have encountered *D. lobipes* at carcasses in March at the peak of the dry season.

The seasonal pattern of appearance and disappearance of the three species of *Dichotomius* was essentially the same in the forest and the pasture, but involved many fewer individuals in the pasture. However, it was striking that on nights following runs of several consecutive hot dry days, the numbers of *Dichotomius* taken in the pasture traps were much more severely depressed than they were in the forest traps (e.g., 10–12 and 26 June).

Dung homogeneity. At the time the dung was put in the traps through the night of 14 June, each trap received dung of slightly different ages and from different horses. At the least, odor, consistency and dryness varied among the bait piles. These traps collected highly variable numbers of beetles, even though the traps were only one meter apart (Tab. 4). Since the bait in the four traps at a site undoubtedly generated a collective odor cue for the beetles, the differences among traps were

Tab. 4. Numbers of *Dichotomius yucatanus* taken in four traps at each of two forest and two pasture sites when the bait in each trap came from a single horse dung pile (not homogenized among traps) and when the dung in each trap was a homogenized mix of dung from many horses (homogenized among traps).

Date	Forest											
	Site AF						Site BF					
Trap	1	2	3	4	sum	CV*	1	2	3	4	sum	CV*
Dung not homogenized among traps:												
June 4	174	663	193	354	1384	0.65	424	510	315	387	1636	0.20
6	422	626	328	454	1830	0.27	641	783	790	1027	3241	0.20
8	623	534	688	513	2358	0.14	815	642	655	581	2693	0.15
10	3	0	0	9	12	1.42	326	198	216	122	862	0.39
12	112	143	252	436	943	0.62	51	141	201	293	686	0.59
14	203	39	59	127	428	0.69	106	75	392	162	735	0.78
Dung homogenized among traps:												
16	382	268	488	331	1469	0.25	503	484	748	625	2360	0.21
18	315	243	181	248	987	0.22	442	510	335	475	1622	0.16
20	424	146	79	264	913	0.66	146	338	151	156	791	0.47
22	420	337	259	461	1477	0.24	559	607	384	717	2267	0.24
24	269	250	204	378	1101	0.27	301	284	233	403	1221	0.23
26	154	270	194	126	744	0.33	263	309	257	143	972	0.29

* CV = coefficient of variation, X̄/s.d.

Date	Pasture											
	Site AP						Site BF					
Trap	1	2	3	4	sum	CV*	1	2	3	4	sum	CV*
Dung not homogenized among traps:												
June 4	46	24	60	72	202	0.41	44	110	109	97	360	0.35
6	53	125	136	39	353	0.56	74	64	201	102	441	0.57
8	66	71	78	26	241	0.39	22	69	123	196	410	0.73
10	9	4	2	10	25	0.62	47	67	59	27	200	0.35
12	1	0	0	1	2	1.15	1	0	0	2	3	1.28
14	103	59	118	27	307	0.54	97	4	4	6	111	1.66
Dung homogenized among traps:												
16	73	97	79	117	366	0.22	64	134	67	79	344	0.38
18	97	59	54	71	281	0.27	41	63	77	20	201	0.50
20	52	26	37	24	139	0.37	16	35	12	30	93	0.47
22	4	6	24	11	45	0.80	17	8	11	12	48	0.31
24	34	16	10	4	64	0.68	7	19	15	16	57	0.36
26	2	1	2	1	6	0.38	4	4	2	6	16	0.41

probably produced by evaluation of the competing odor cues once the beetles were close enough to distinguish among the four traps. To examine the impact of different dung origin on trap attractiveness, after 14 June the dung was homogenized before baiting all traps. The collection results for *Dichotomius yucatanus* given in Tab. 4 after 14 June appear to be more uniform among traps at a site than for the six previous nights. To examine this, a Coefficient of Variation (CV = mean/s.d.) was calculated for each night at each site (Tab. 4). The grand mean of all the CV's for 4–14 June (0.63, s.d. = 0.40) is nearly twice as large as that for 16–26 June (0.36, s.d. = 0.16) ($t_{46\ d.f.} = 2.82$, $p < 0.01$). Since the control (4–14 June) for the experiment (16–26 June) is retroactive, these results are at best weak evidence, but they are consistent with the idea that homogenization of dung reduces the variation among traps within a trapping site.

Discussion

This survey of dung beetle arrival at traps baited with fresh horse dung shows clearly that there is very strong seasonal heterogeneity in the presence of adult nocturnal large dung beetles and that this heterogeneity is not equally contributed to by all the species. It is striking that it was the largest and the smallest (the rarest and the commonest), *Dichotomius* species that had the same seasonal pattern of adult abundance and thus dung harvest. Teneral adult *D. centrale* were present at low densities throughout the first four months of the rainy season, followed by strong appearance at dung about the time that *D. yucatanus* and *D. carolinus* had largely disappeared. It is tempting to suggest that this is yet another example of genetically-programmed temporal displacement of closely related species using the same resource, coupled with major differences in size and abundance between those that are synchronous in seasonal activity (for an extratropical example with dung beetles, se Hanski and Koskela 1979). Likewise, it is striking that *Copris lugubris,* a beetle of about the same size as a large *D. yucatanus* or a small *D. centrale,* showed no large seasonal peak in activity within the rainy season.

An alternative hypothesis has been suggested for the strong seasonal difference in abundance between *D. centrale* adults and the other two *Dichotomius* (H. F. Howden, pers. comm.). It is possible that *D. centrale* avoids dung being mined by *D. yucatanus* and therefore usually avoided the traps until the density of *D. yucatanus* had fallen substantially in early September. That the *D. centrale* numbers in the traps did not increase during the occasional lows in *D. yucatanus* numbers is not a natural test of the hypothesis since the same physical environment factors that are inimical to *D. yucatanus* adult activity may also depress *D. centrale* adult activity.

The results of the survey suggest that *D. centrale* is by and large a forest dung beetle. Not only was its ratio of forest numbers to pasture numbers of individuals the greatest among all the species, but site AP contributed about 60% of the beetles in the pasture (Tab. 2); site AP was only 20 m from the forest edge while site BP was about 50 m from the forest. Additionally, at Santa Rosa *D. centrale* is encountered only very rarely in dung placed hundreds of meters out into large pastures. *D. carolinus* and *D. yucatanus* show no such diminution of density in dung far from forest, and it is tempting to think of them as 'grassland species' (and *D. carolinus* has been labeled as such by Halffter and Matthews 1966). However, the fact that 6.6 to 4.2 times as many of them were taken in the forest traps as in the grassland traps suggests that they are also forest animals but will move readily into open grasslands (pastures) for dung. Since this area of Central America lacked large numbers of post-Pleistocene large herbivores and natural grasslands before introduction of Western ranching practices, these beetles must have survived as forest species or be recent invaders from other parts of Central America.

D. yucatanus and *D. carolinus* probably have but one generation per year, since almost no teneral adults were encountered after late May. Since vertebrate dung is likely to be about as common in the second half of the rainy season as in the first (and indeed, supports the population of *D. centrale* at that time), I suspect that the absence of a second generation is due to a long developmental time of the larvae on a diet of dung. However, it appears that *D. centrale* remains underground until the population of *D. yucatanus* and *D. carolinus* adults have finished provisioning their nests. Such behavior implies that more resources are available to *D. centrale* in the second half of the rainy season than in the first half. It appears that *D. yucatanus* and *D. carolinus* are responsible for this resource heterogeneity since they process most of the dung in the first half of the rainy season. Alternatively, as mentioned before, *D. centrale* may be present but not using the dung heavily occupied by *D. yucatanus.*

The absence of adults of all the large dung-eating Scarabaeinae (except *Deltochilum lobipes* which also takes carrion) during the Santa Rosa dry season (at least January-April) is probably due to the difficulty of digging a deep tunnel through the dry hard ground. The dung of both horses and cattle simply accumulates during the dry season, and then rots very quickly when the first rains come; the large dung beetles discussed here show no interest in the old dung that is newly wetted by the first rains. Santa Rosa lacks the large fauna of dung-degrading termites that removes much dry season dung in East Africa (Coe 1977).

The large nocturnal dung beetles were conspicuous in not emerging from the soil the night of the first heavy rain. I suspect that they have to wait for the moisture to soak down to them as a cue, or to soften the soil so that they can burrow out, or both.

The strong seasonality of the major dung-harvesting scarabs at Santa Rosa has implications for much more than termites and other animals that feed on the dung that falls and dries in situ during the dry season. The dry season is a major time of consumption of tree fruits by horses (and cattle) and their dung is often rich in seeds during the second half of the dry season and for a mouth or more after the rain starts. The seeds are harvested by forest mice acting largely as seed predators (Janzen 1982b, c). They harvest many of the seeds during the first few nights after the dung falls. When there is a heavy infestation of large dung beetles in a pile of horse dung, there is the chance that some seeds will be buried or fall down beetle tunnels before the rodents can harvest them. During the dry season, no such interference is possible and the mice may harvest a larger fraction of the seeds in the dung. Even during the second half of the rainy season, the possibility of dung beetle 'rescue' of seeds is reduced since the number of *D. centrale* that arrives at a dung pile is substantially less than the number of *D. yucatanus* and *D. carolinus* in the first half of the rainy season, and dung degradation is much less thorough.

The Santa Rosa dung beetle fauna is probably a mere remnant of what was once supported by the Pleistocene megafauna. With the extinction of ground sloths, gomphotheres, glyptodonts, horses, etc., the dung beetles that survived would have been those that could survive on the very diffuse and small-particle dung rain that is generated by humans and the many small species of vertebrates in a tropical deciduous forest. With the introduction of a cow and horse megafauna, the dung beetles have again a resource that comes in 1–2 kg packets in large numbers. However, it should be a long time before the species richness again climbs to the level that was probably supported by the Pleistocene megafauna, since there is no nearby source area with a rich fauna of large dung beetles from which more species may immigrate. Likewise, a more complex dung beetle fauna supported by a more varied and larger rain of large mammal dung should have contained more dung beetle life-forms than are presently in the Santa Rosa forest. Under these circumstances, there may well have been numerous specialists at using dung in the dry season and the three species of *Dichotomius* may well have been sharing the world in a more complex manner with many more species of dung beetles. The distribution of *Dichotomius,* as well as that of *Copris lugubris,* on the Santa Rosa dung may be hardly more than an ecological pattern generated by the movement of forest dung beetles into horse- and cattle-rich pasture and forest mosaics over the past 300 yr, with little or no evolutionary change in the beetles.

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