Journal of Tropical Ecology (1993) 9:45–54. With 5 figures

Dung beetles attracted to mammalian herbivore (*Alouatta palliata*) and omnivore (*Nasua narica*) dung in the tropical rain forest of Los Tuxtlas, Mexico.

ALEJANDRO ESTRADA, GONZALO HALFFTER*, ROSAMOND COATES-ESTRADA *and* DENNIS A. MERITT JR†

Estacion de Biologia 'Los Tuxtlas', Instituto de Biologia-UNAM, Apartado Postal 176, San Andres Tuxtla, Veracruz, Mexico.
* *Instituto de Ecologia, A.C., Apartado 43, Xalapa, Mexico.*
† *Lincoln Park Zoological Society, 2200 N. Cannon Drive, Chicago, Ill. 60614, USA.*

ABSTRACT. Dung beetles attracted to howler monkey (*Alouatta palliata*) and coati (*Nasua narica*) dung were studied for an annual cycle in the tropical rain forest of Los Tuxtlas, Mexico. Pitfall traps set for 24 h month^{-1} captured 1567 dung beetles of 21 species. The species *Canthidium martinezi*, *Deltochilum pseudoparile* and *Canthon femoralis* accounted for 62% of all individuals captured. While species overlap was high (> 80%) between diurnal and nocturnal samples and between howler monkey and coati dung baits, coati dung attracted species such as *C. martinezi*, *D. pseudoparile* and *Onthophagus rhinolophus* while species such as *C. femoralis* and *Copris laeviceps* were numerically dominant at howler monkey dung. Thirteen non-ball rolling dung beetle species and eight ball-rolling species accounted for 43% and for 57% of all beetles captured respectively. Dung beetles were present and active in all months of the year, but occurred in higher numbers between the months of March and October, when temperatures were higher. Relative abundance of howler monkey and coati dung in the rain forest of Los Tuxtlas was estimated at 11.2 g (fresh weight) ha^{-1} day^{-1} and at 13.0 g ha^{-1} day^{-1} respectively, a seemingly low amount for the large number of scarabs attracted to the dung.

KEY WORDS: *Alouatta Palliata*, dung beetles, Mexico, *Nasua narica*, Scarabaeidae, tropical rain forest.

INTRODUCTION

Dung beetles are conspicuous in tropical rain forests (Halffter & Matthews 1966, Hanski 1983, 1989, Howden & Nealis 1975, 1978, Howden & Young 1981, Peck & Forsyth 1982) and use the dung produced by forest vertebrates, particularly herbivores such as primates, and occasionally that of birds and reptiles (Howden & Young 1981, Young 1981) as food and as a substrate for oviposition and further feeding by their larvae (Halffter & Edmonds 1982, Gill 1991, Hanski 1989). Carrion and decaying fruit and fungi are also used as sources of food (Halffter & Matthews 1966, Hanski 1989). Field studies have suggested or implied that dung resources in the tropical rain forest are limited as a result of the general scarcity and patchy distribution of dung-producing mammals and dung beetles compete intensively for resources as attested by their competitive and combative behaviours (Halffter & Edmonds 1982, Hanski 1991), but quantitative evidence is lacking in the literature (but see Giller & Doube 1989). Resource partitioning such as preference for soil and cover (Lumaret 1978, Nealis 1977), diel flight time and dung size (Peck & Howden 1984), perching heights (Howden & Nealis 1978) and dung removal methods (Halffter & Matthews 1966) has been noted, but quantitative information on preferences by dung beetles for particular types of dung is scanty for the Neotropical rain forest (but see Hanski 1989, Gill 1991).

Seasonal changes appear less pronounced in dung and carrion beetles (Janzen 1983, Moron & Terron 1984, Moron *et al* 1985, Walter 1978) than in many other insects as availability of dung and carrion is less seasonal than for other resources (Hanski 1989). Quantitative data on seasonal abundance of dung beetles has only been reported for a few tropical localities, namely Sarawak (Hanski 1983), Panama (Young 1978, Wolda & Estribi 1985), Colombian Amazon (Howden & Nealis 1975), Brazil (Waage & Best 1985) and the Ivory Coast (Cambefort 1982). But for tropical wet forests in the Neotropics no overt seasonality was observed in Ecuador (Peck & Forsyth 1982).

In Neotropical rain forests, herbivore dung such as that of howler monkeys (*Alouatta* spp.) has been reported to be a preferred resource for several dung beetle species (Halffter & Edmonds 1982, Howden & Young 1981, Peck & Forsyth 1982). However, systematic data on beetle preference for dung of rain forest mammals differing in feeding habits are virtually non existent.

In this paper we present data on species richness, composition and seasonality of the dung beetle community attracted to howler monkey (*Alouatta palliata* Gray) and coati (*Nasua narica* Linnaeus) dung in the tropical rain forest of Los Tuxtlas, Veracruz, Mexico. The diet of the howler monkey is strictly plant-based whereas, the coati diet is, in general, omnivorous (Coates-Estrada & Estrada 1986).

METHODS

Monthly trapping of dung beetles was conducted between January and December 1988 within the lowland evergreen tropical rain forest of the biological station Los Tuxtlas (700 ha) of the Instituto de Biologia of UNAM in southern Veracruz, Mexico (95° 04′ W, 18° 34′ N, elevation 150–530 m). This forest is the northernmost example of the ecosystem in the American continent. Mean annual rainfall is 4900 mm with a dry season ($\bar{X}$ = 111.7 SD ±11.7 mm month^{-1}) from March to May and a wet season ($\bar{X}$ = 486.25 SD ±87.0 mm month^{-1}) from June to February. Mean annual temperature is 25°C (range 20–28°C). Howler monkeys and coatis are conspicuous mammal species in this rain forest (Coates-Estrada & Estrada 1986).

One hundred pitfall traps (similar to those described in Howden & Nealis 1975) were used. Fifty were baited with 20 g of fresh howler monkey dung and

50 with coati dung. They were arranged in 25 mixed pairs in two rows 5 m apart, each pair being placed at 20 m intervals along a 500 m belt transect. Traps were operated for one continuous 24 h period in each of 12 consecutive months. Fresh bait was placed at 0600 h, traps were emptied and bait renewed at 1800 h, and again at 0600 h the next morning. Because change-over times inevitably straddle the activity times of diurnal and nocturnal species, diurnal species turned up in the nocturnal traps and vice versa (see below). The mean (± SD) interval between trapping sessions was 25 (± 3.0) days. All beetles were identified to species and their fresh weight recorded. Biomass in this report refers to fresh weight.

RESULTS

Species richness

A total of 1567 beetles of 21 species were collected during this study. The assemblage for these two types of dung was strongly dominated by five species accounting for 81% of all individuals captured. Two species *Canthidium martinezi* (28%) and *Deltochilum pseudoparile* (23%) were particularly dominant. *Canthon femoralis* represented 11% of the total number of individuals (Table 1). Authorities for species are in Table 1.

Nocturnal v. diurnal

While the nocturnal traps yielded 19 species, 18 species were captured in the diurnal traps (Table 1). Species overlap between diurnal and nocturnal captures was 87%, some of which was probably due to the straddling of species when changing baits between diurnal and nocturnal periods. Based on ratios of abundance in diurnal versus nocturnal traps, the following species showed clear nocturnal or diurnal activity, in both dung types (Table 1). Three species in the nocturnal traps accounted for 82% of all records: *C. martinezi* (38%), *D. pseudoparile* (32%) and *Copris laeviceps* (12%). These species occurred in significantly higher numbers in the nocturnal than in the diurnal traps (*C. martinezi* $X^2 = 350.5$, $P < 0.001$; *D. pseudoparile* $X^2 = 298.8$, $P < 0.001$; and *C. laeviceps* $X^2 = 84.8$, $P < 0.001$). Six species were captured significantly more often in the diurnal traps. Of these *C. femoralis* contributed to 33% of the total diurnal sample (Table 1). A Spearman rank correlation coefficient between the ranks of species detected in diurnal traps and their rank in the nocturnal traps yielded a non significant value ($r_s = 0.33$ NS) thus suggesting a difference in the structure of these segments of the dung beetle community.

Effect of bait

Of all the beetles collected (19 species), 57% were in coati dung, and 43% (17 species) in howler dung. (Tables 2, 3). The three most common species attracted to coati dung traps were *D. pseudoparile* (34%), *C. martinezi* (29%), and *Onthophagus rhinolophus* (12%) (Table 2). The three most common species at howler dung

Table 1. Total number of species of dung beetle attracted to coati and howler monkey dung pitfall traps. Diurnal/nocturnal/(D/N) determined from the evenness of captures.

Species	Diurnal	Nocturnal	Total	Roller	D/N
Canthidium martinezi Halffter & Matthew	22	412	434		N
Deltochilum pseudoparile Paulian	23	342	365	R	N
Canthon femoralis Chevrolat	161	6	167	R	D
Copris laeviceps Harold	18	130	148		N
Onthophagus rhinolophus Harold	57	76	133		?
Dichotomius satanas Harold	4	55	59		N
Canthon sp. 1	42	8	50	R	D
Canthon viridis Martinez, Halffter & Halffter	48	2	50	R	?
Eurysternus mexicanus Harold	33	4	37		D
Canthon cyanellus LeC.	28	0	28	R	D
Phanaeus endymion Harold	21	6	27		D
Sulcophanaeus chryseicollis Harold	19	2	21		D
Coprophanaeus telamon Harold	1	16	17		N
Onthophagus batesi Howden & Cartwright	4	6	10		?
Deltochilum gibbosum Fabricius	1	4	5	R	?
Uroxys boneti Westwood	0	5	5		?
Canthon subhyalinus Harold	2	1	3	R	?
Onthophagus nasicornis Harold	1	2	3		?
Canthon sp. 2	0	2	2	R	?
Dichotomius carolinus (Say)	0	2	2		?
Anaides laticollis Harold	0	1	1		?
Total	485	1082	1567		
Total species	18	19	21		

Table 2. Dung beetles attracted to coati dung pitfall traps. Full scientific names are given in Table 1.

Species	Diurnal	Nocturnal	Total	Roller	Diur/Noct
D. pseudoparile	9	288	297	R	N
C. martinezi	13	247	260		N
O. rhinolophus	45	59	104		?
C. laeviceps	1	60	61		N
C. viridis	42	1	43	R	D
C. cyanellus	23	0	23	R	D
D. satanas	2	17	19		N
C. telamon	1	16	17		N
P. endymion	14	3	17		D
Canthon sp. 1	10	4	14	R	D
O. batesi	3	6	9		?
C. femoralis	7	0	7	R	D
D. gibbosum	1	4	5	R	?
E. mexicanus	4	0	4		?
C. subhyalinus	1	1	2	R	?
O. nasicornis	1	1	2		?
A. laticollis	0	1	1		?
Canthon sp. 2	1	0	1	R	?
D. carolinus	0	1	1		?
Total	178	709	887		
Total species	17	15	19		

traps were *C. martinezi* (26%), *C. femoralis* (24%), and *C. laeviceps* (13%) (Table 3). Most of the beetles (80%) were captured from coati traps overnight but only a small difference was observed between day and night catches (45% v. 55%) in howler dung (Tables 2, 3). No correlation was found between overall species composition in coati and howler traps (Spearman $r_s = 0.35$ NS) suggesting that, overall, the structure of the assemblages was different.

Species showing a significant preference for coati dung were *C. martinezi* ($X^2 = 17.0$, $P < 0.001$), *D. pseudoparile* ($X^2 = 143.7$, $P < 0.0001$) and *O. rhinolophus* ($X^2 = 42.3$, $P < 0.001$). In contrast, species preferring howler dung were *C. femoralis* ($X^2 = 140.2$ $P < 0.001$), *Eurysternus mexicanus* ($X^2 = 22.7$, $P < 0.001$), *Dichotomius satanas* ($X^2 = 7.5$, $P. < 0.01$). *Canthon* sp. 1 ($X^2 = 9.6$ $P < 0.01$) and *C. laeviceps* ($X^2 = 4.5$, $P < 0.05$) Table 2.

Table 3. Dung beetles attracted to howler dung pitfall traps. Full scientific names are given in Table 1.

Species	Diurnal	Nocturnal	Total	Roller	Diur/Noct
C. martinezi	9	165	174		N
C. femoralis	154	6	160	R	D
C. laeviceps	17	70	87		N
D. pseudoparile	14	54	68	R	N
D. satanas	2	38	40		N
Canthon sp. 1	32	4	36	R	D
E. mexicanus	29	4	33		D
O. rhinolophus	12	17	29		?
S. chryseicollis	19	2	21		D
P. endymion	7	3	10		?
C. viridis	6	1	7	R	?
C. cyanellus	5	0	5	R	?
U. boneti	0	5	5		?
Canthon sp. 2	1	0	1	R	?
C. subhyalinus	1	0	1	R	?
D. carolinus	0	1	1		?
O. batesi	1	0	1		?
O. nasicornis	0	1	1		?
Total	309	371	680		
Total species	15	14	17		

Ball-rolling and non ball-rolling dung beetles

Eight species of ball-rolling dung beetles were captured in the pitfall traps accounted for 13 species and for 57% of all individuals captured; *C. martinezi*, (54%) and *C. femoralis* (25%) accounted for 79% of all ball-rolling dung beetles captured (N = 670). *D. pseudoparile* numerically dominated (76% of all ball-rolling beetles captured) the traps baited with coati dung, and *C. femoralis* dominated (57%) the samples in howler dung raps. Non ball-rolling beetles accounted for 13 species and for 57% of all individuals captured. *C. martinezi*, accounted for 48% of all non ball-rolling beetles captured and two other species, *C. laeviceps* and *O. rhinolophus*, accounted for an additional 30% (Tables 2,3).

Seasonal occurrence of dung beetles at pitfall traps

Addition of new species in the monthly samples were slow between January and March but increased in April at which time 95% of all species detected had been captured. Dung beetles were present and active in all months of the year, but occurred in higher numbers between the months of March and October when mean monthly temperatures are higher (Figure 1). The mean (± SD) number of species of dung beetles captured per 24 hour/month sample was 11.5 (± 3.3; range 6–18). The mean (± SD) number of species and individuals captured per month in the coati and howler dung pitfall traps was 8.5 (± 3.4), 73.9 (± 35.1) and 8.1 (± 2.5). 56.6 (± 34.5) respectively (Figure 1). A clear peak of abundance was found in April in both dung types and a second peak in August and September in the howler traps (Figure 1). Dung beetle biomass ranged from 0.80 g (February) to 12.6 g (August). Biomass values showed an increase after February reaching a maximum peak (19%) in August and a secondary peak (12.9%) in October.

Dung availability

As regular consumers of leaves, howler monkeys have a long gut clearance time ranging from 12–20 h (Estrada & Coates-Estrada 1984). Our field observations on howler monkey faecal deposition showed that there was one every 10–12 h per individual. Average troop size at Los Tuxtlas was 9.0 individuals resulting in an estimated 18 faecal deposits per 24 h period for the average troop. On average, each faecal deposit weighs (fresh weight) 25 g (range 14–35 g; N = 200) which yields a total production of 450 g of fresh faecal matter day^{-1}. The average home range size is 40 ha (range 30–60; intertroop home range overlap about 5%) which yields a distribution of only 11.2 g of fresh faecal matter ha^{-1} day^{-1} in the forest (Estrada 1982).

In the case of the coati, our field data indicated a mean band size of 22.5 individuals (range 10–25; N = 8), an average number of faecal deposits per individual per 24 h of 2.5 and a mean fresh weight of 18 g per faecal expulsion. This results in an estimated 1040.6 g of fresh faecal matter day^{-1}. The average home range size of coati bands at Los Tuxtlas is 80 ha (range 50–110; interband home range overlap about 5–10%) which results in 13.0 g of fresh faecal matter ha^{-1} day^{-1} (AE unpublished data).

DISCUSSION

While our study consisted of only 24 h monthly samples, it is noteworthy that only six of the 27 species reported for the Los Tuxtlas rain forest (Moron 1979) were undetected by our sampling using the two types of dung. Since several dung beetle species may have crepuscular diel activity, our study has overestimated the overlap in diel activity. In addition, howler monkeys and coatis are not the only mammals in the rain forest of Los Tuxtlas and it is possible that dung beetles may be attracted to resources produced by some of the other mammal

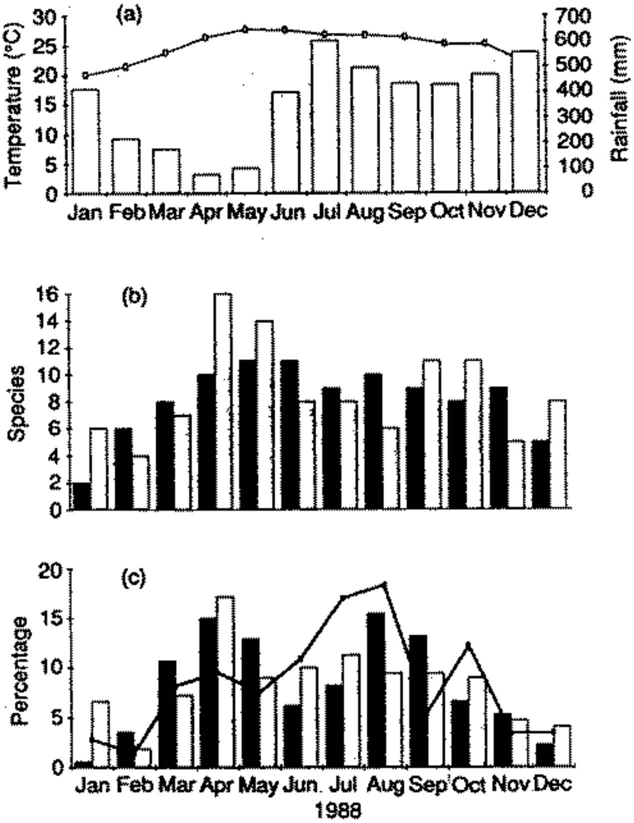

Figure 1. (a) Monthly rainfall and mean monthly temperature at the study site, 1988, (b) monthly records of dung beetle species at howler monkey (shaded bar) and coati dung pitfall traps, (c) percentage of individuals captured at howler monkey (N = 680) and coati (N = 887) dung pitfall traps. The continuous line is the percentage biomass (fresh weight) of dung beetles captured each month.

species occurring in this locality. Be that as it may, our study in the rain forest of Los Tuxtlas showed that the dung beetle community attracted to both howler monkey and coati dung is numerically dominated by the species *C. martinezi*, *D. pseudoparile* and *C. femoralis*. Diurnal samples were particularly dominated by *C. femoralis* and nocturnal samples were dominated by *C. martinezi* and *D. pseudoparile*.

Coati dung was particularly attractive to species such as *C. martinezi*, *D. pseudoparile* and *O. rhinolophus*, while howler monkey dung attracted species such as *C. femoralis* and *C. laeviceps*. An examination of segregation by photoperiod and dung type revealed that the beetle community at coati dung traps was dominated by two species active at night (*D. pseudoparile* (42%) and *C. martinezi* (37%). In the case of howler dung, *C. femoralis* dominated the diurnal samples (50%) and several species such as *C. martinezi* (44%), *C. laeviceps* (19%) and *D. satanas* (10%) dominated the nocturnal samples. These data suggest a finer segregation in resource exploitation given by activity period and resource specificity than previously demonstrated.

Animal dung is not the only resource used by dung beetles in tropical forests. Carrion and rotting fruit are used concurrently by many of the species we found to be attracted to howler monkey or coati dung (Halffter & Matthews 1966). It is possible that low food availability and intense competition render strict specialization on a particular resource of limited value (Hanski 1989, 1991). Specialization is apparently more pronounced when nesting. For example, *Canthon cyanellus* can be found in either dung or carrion, but nests only in carrion (G. Halffter, personal observations). Species segregation occurs also in flight height. *Canthon femoralis* can be captured in significantly higher numbers (tenfold) at heights of 10 m, which presumably has a relationship with the affinity displayed by this beetle for monkey dung (Peck & Howden 1984). Species preferences for dung type were evident in this study. For example, *D. pseudoparile* was significantly more common at coati dung, while *C. femoralis* was significantly more common at howler dung.

In contrast to the aseasonal activity in dung beetles in an Ecuadorian rain forest with no severe dry season reported by Peck & Forsyth (1982), dung beetle abundance in the rain forest of Los Tuxtlas displayed a bimodal distribution over the year possibly related to changes in temperature, rainfall, adult emergence and, possibly, fruit availability. While the number of species appearing in the monthly captures at howler dung showed little variation, a bimodal pattern in species occurrence at coati dung was evident. The number of individuals captured at both types of dung differed in the pattern of appearance in the monthly samples, with a clear bimodal pattern for dung beetles attracted to howler dung. To what extent these features may be related to a seasonal distribution of dung resources is at present unknown.

The prediction that dung is a limited resource to dung beetles (Hanski 1989) is supported by the present study. The estimated availability of 11.2 g and 13.0 g of fresh faecal matter ha^{-1} day^{-1} of howler monkey and coati dung respectively, indicated a very low density of dung available for the numbers of dung beetles and species attracted to this resource. Discovery times are short with beetles arriving at dung deposition clumps within 1 min during the day and dung burial rates have been documented to be less than 2 h (Peck & Forsyth 1982, AE personal observations). Diurnal and nocturnal activity, along with differences in foraging methods, may reduce the intense competition usually observed among dung beetle species (Hanski & Cambefort 1991a,b).

The dependence of dung beetles on resources produced by particular vertebrate components in tropical rain forests and the high sensitivity of these animals to the rapid destruction and fragmentation of the Neotropical rain forests, resulting in the alteration of number and species occurrence and distribution and/or in species extinction may indicate the likelihood of important changes in the composition and structure of the dung beetle community hitherto little documented.

ACKNOWLEDGEMENTS

This research was supported by UNAM, the Lincoln Park Zoological Society of Chicago and The Explorer's Club of New York. We thank two anonymous reviewers for helpful suggestions.

LITERATURE CITED

CAMBEFORT, Y. 1982. Les coleopteres Scaracidae s. str. de Lamto (Cote d'Ivore): structure des peuplements et role dans l'ecosysteme. *Annales Societe Entomologique de France* (N.S.) 18:433–459.

COATES-ESTRADA, R. & ESTRADA, A. 1986. *Manual de Identification de Campo de los Mamiferos de la Estacion de Biologia 'Los Tuxtlas'*. Universidad Nacional Autonoma de Mexico. Mexico, D.F.

ESTRADA, A. 1982. Survey and census of howling monkeys (*Alouatta palliata*) in the tropical rain forest of Los Tuxtlas, Veracruz, Mexico. *American Journal of Primatology* 2:363–372.

ESTRADA, A. & COATES-ESTRADA, R. 1984. Fruit eating and seed dispersal by howling monkeys (*Alouatta palliata*) in the tropical rain forest of Los Tuxtlas, Veracruz, Mexico. *American Journal of Primatology* 6: 77–91.

GILL, B. D. 1991. Dung beetles in tropical American forests. Pp. 211–299 in Hanski, I. & Cambefort, Y. (eds). *Dung beetle ecology*, Princeton University Press. Princeton, New Jersey.

GILLER, P. S. & DOUBE, B. M. 1989. Experimental analysis of inter and intraspecific competition in dung beetle communities. *Journal of Animal Ecology* 58:129–142.

HALFFTER, G. & EDMONDS, W. D. 1982. *The nesting behavior of dung beetles (Scarabaeinae): an ecological and evolutive approach*. Instituto de Ecologia, A. C., Mexico, D. F.

HALFFTER, G. & MATTHEWS, E. G. 1966. The natural history of dung beetles of the subfamily Scarabaeinae (Coleoptera, Scarabaeidae). *Folia Entomologica Mexicana* 12–14:1–312.

HANSKI, I. 1983. Distributional ecology and abundance of dung and carrion-feeding beetles (Scarabaeidae) in tropical rain forest in Sarawak, Borneo. *Acta Zoologica Feenica* 167:1–45.

HANSKI, I. 1989. Dung beetles. Pp. 489–511 in Lieth, H. & Werger, M. J. A. (eds). *Tropical rain forest ecosystems*. Elsevier Science Publishers B. V., Amsterdam.

HANSKI, I. 1991. Dung insect community. Pp. 5–21 in Hanski, I & Cambefort, Y. (eds). *Dung beetle ecology*. Princeton University Press, Princeton, New Jersey.

HANSKI, I. & CAMBEFORT, Y. 1991a. Species richness. Pp. 350–365 in Hanski, I. & Cambefort, Y. (eds). *Dung beetle ecology*, Princeton University Press, Princeton, New Jersey.

HANSKI, I & CAMBEFORT, Y. 1991b. Resource partitioning. Pp. 331–349 in Hanski, I. & Cambefort, Y. (eds). *Dung beetle ecology*, Princeton University Press, Princeton, New Jersey.

HOWDEN, H. F. & NEALIS, V. G. 1975. Effects of clearing in a tropical rain forest on the composition of the coprophagous scarab beetle fauna (Coleoptera). *Biotropica* 7:77–85.

HOWDEN, H. F. & NEALIS, V. G. 1978. Observations on height of perching in some tropical dung beetles (Scarabeidae). *Biotropica* 10:43–46.

HOWDEN, H. F. & YOUNG, O. P. 1981. Panamanian Scarabaeidae. *Contributions to the American Entomological Institute* (Ann Arbor, Michigan) 18:1–204.

JANZEN, D. H. 1983. Seasonal change in abundance of large nocturnal dung beetles (Scarabaeidae) in a Costa Rican deciduous forest and adjacent horse pasture. *Oikos* 41:274–283.

LUMARET, J. P. 1978. Biogeographie et ecologie des Scarabaeides coprophages du sud de la France. *Vie Milieu* 28 (ser. C)1–34.

MORON, M. A. 1979. Fauna de coleopteros lamelicornios de la Estacion de Biolgia Tropical "Los Tuxtlas", Veracruz, UNAM, Mexico. *Anales del Instituto de Biologia*, UNAM, Mexico. 50:375–454.

MORON, M. A. & TERRON, R. A. 1984. Distribucion altitudinal y estacional de los insectos necrofilos en la sierra norte de Hidalgo, Mexico. *Acta Zoologica Mexicana*. (N.S.) 3:1–47.

MORON, M. A., VILLALOBOS, F. J. & DELOYA, C. C. 1985. Fauna de coleopteros lamelicornios de boca de chajul, chiapas, Mexico. *Folia Entomologica Mexicana*. 66: 57–118.

NEALIS, V. G. 1977. Habitat association and community analysis of south Texas dung beetles (Coleoptera: Scarabaeidae). *Canadian Journal of Zoology* 55:138–147.

PECK, S. B. & FORSYTH, A. 1982. Composition, structure and competitive behavior in a guild of Ecuadorian rain forest dung beetles (Coleoptera, Scarabaeidae). *Canadian Journal of Zoology* 60:1624–1634.

PECK, S. B. & HOWDEN, H. F. 1984. Response of a dung beetle guild to different sizes of dung bait in a Panamanian rain forest. *Biotropica* 16:235–238.

WAAGE, J. K. & BEST, R. C. 1985. Arthropod associates of sloths. Pp. 329–332 in Montgomery, G. G. (ed.). *The evolution and ecology of armadillos, sloths and vermilinguas*, Smithsonian Institution Press, Washington, DC.

WALTER, P. 1978. Recherches ecologiques et biologiques sur le Scarabeides coprophages d'une savane du Zaire, These Dr. Pp 360 Universite des Sciences et Techniques du Languedoc. Montpellier, France.

WOLDA, H. & ESTRIBI, M. 1985. Seasonal distribution of the large sloth beetle *Uroxys gorgon* Arrow (Scarabaeidae: Scarabaeinae) in light traps in Panama. Pp. 319–322 in Montgomery, G. G. (ed.). *The evolution and ecology of armadillos, sloths and vermilinguas*, Smithsonian Institution Press, Washington D.C.
YOUNG, O. P. 1978. Resource partitioning in a Neotropical necrophagous scarab guild. Pp. 228. PhD Thesis. The University of Maryland.
YOUNG, O. P. 1981. The attraction of neotropical Scarabaeinae (Coleoptera, Scarabaeidae) to reptile and amphibian fecal material. *The Coleopterists Bulletin* 35:345–348.

Accepted 2 July 1992

Book review

VON WILLERT, D. J., ELLER, B. M., WERGER, M. J. A., BRINCKMANN, E. & IHLENFELDT, H.-D. 1992. *Life strategies of succulents in deserts. With special reference to the Namib Desert.* Cambridge University Press, UK. xix + 340 pages. ISBN 0–521–24468–4. Price: £50.00/$89.95 (hardback).

This book has rather diverse goals which gives it both its charm and difficulties. It is designed to be used by co-workers in the field, also as a textbook, and finally by lay persons interested in this fascinating group of plants. It probably would not totally satisfy any one of these diverse audiences. The text extends from the very general, in the case of the background information on energy balance and water relations, to the considerable and very specific, and principally unpublished results on succulents of South Africa. It is the middle ground of synthesis of the behaviour of succulents globally that is lacking.

There are five sections to the book: a discussion of the nature of succulents, the climate of deserts and the life cycles of desert plants, the nature of the Namib desert specifically, the physiological responses of succulents (which makes up the bulk of the book), and a discussion of life strategies of succulents. The physiological discussions centre on the nature of Crassulacean acid metabolism (CAM) and its ecological significance with the rather surprising conclusion of 'the more facts we know about succulents with and without CAM the more difficult it becomes to evaluate the ecological relevance of CAM'. Other investigators in this field may not share this pessimistic view.

This very handsome volume makes a natural companion to Park Nobel's book on the '*Environmental biology of agaves and cacti*' produced by the same publisher.

H. A. Mooney
Department of Biological Sciences, Stanford University, Stanford, California 94305, USA