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Nocturnal Perching of Scarabaeine Dung Beetles (Coleoptera, Scarabaeidae) in an Australian Tropical Rain Forest[1]

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ABSTRACT

Wongabel, a northeastern Queensland tropical, wet, evergreen forest, contains 22 species of Scarabaeinae dung beetles. Five of these species were observed to perch commonly on leaves at night. Length of the beetle and the height of its perch were recorded for each of 561 specimens. Unlike the New World tropical dung beetle perchers, no clear evidence was found that small species perched closer to the ground than larger species. The evidence gathered, at least for the four most common perchers, supports the hypothesis that perching is one type of foraging strategy. The similarities and differences between the Australian and New World perchers are discussed.

THE NUMBER OF SPECIES OF SCARABAEINE DUNG BEETLES increases from temperate to tropical areas (Howden 1985) and there is a concomitant increase in the diversity of behavioral responses to food resources. One type of behavior that is rarely seen outside of tropical, wet forests is perching near the ground on leaves of understory plants. The typical alert posture of a perching scarabaeine includes standing with the body somewhat elevated above the surface of the leaf with the antennae extended, the lamellae flared, and the body oriented in the same compass direction as nearby specimens. Howden and Nealis (1978) discussed this perching phenomenon and showed that in Ecuadorian tropical forests species of small (3–4 mm) scarabaeine dung beetles perched close to the ground and larger species (5–9 mm) perched progressively higher to a maximum height of about a meter. Beetles over 10 mm in length were rarely seen perching. It was suggested that perching rather than flying was one possible method of locating small-sized food resources (dung). Howden and Nealis (1978) also noted that some species of perchers were active at night, and Gill (1986) subsequently found that times of perching may differ for different species at various times of both day and night. Peck and Howden (1984) found, for a wet forest in Panama having a fauna of 28 species, that six species came only to small (2 cc) deposits of feces and never to large (200 cc) deposits of the same dung. Those species that came only to the small deposits were the common perchers, thus supporting the hypothesis that perching was a type of foraging strategy. Other theories explaining why some species perch, for example for thermoregulation, are discussed by Gill (1986), but none of these non-foraging theories explain nocturnal perching.

In 1975, two of us (ATH and HFH) noted that nocturnal scarab perching occurred in a tropical rainforest near Atherton, northeastern Queensland. No perching scarabaeines were observed in Australia in 19 months of subsequent field work in cool temperate rainforests of eastern and western Australia as well as in open sclerophyll habitats. The perching habit apparently regularly occurs only in rainforests (tropical, wet, evergreen forests), which in Australia are found mostly in northeastern Queensland.

In 1988–89, we revisited the patch of rainforest near Atherton and investigated the diversity and behavior of its scarabaeine dung beetle fauna. The purpose of this paper is to describe this behavior and compare it to that of tropical New World perching scarabaeines.

METHODS

STUDY AREA.—Wongabel State Forest is located 8 km south of Atherton, Queensland, at 17°19′S, 145°28′E. It contains 639 hectares with an average elevation of 760 m. Fifty percent of the forest is in plantations, mostly of native hoop pine (*Araucaria cunninghamii* Aiton ex. D. Don); the remaining

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area consists mostly of evergreen rainforest. The region has an average December–January maximum temperature of 28.5°C, minimum 17.7°C, and an average annual rain fall of 1405 mm which occurs mostly between December and March. In Wongabel there are over 10 km of tracks and a 2.6 km "botanical walk" with 190 identified trees. Within the forest and along the tracks there are many low seedlings and herbaceous plants. One of the most common is a smooth-leaved *Ixora* sp., probably *I. biflora* Fosb. (Rubiaceae). Living in the forest are nine species of small marsupials, four species of rodents, a number of bats including flying-foxes, and a few feral pigs (L. A. Moore, pers. comm.).

DATA COLLECTION.—One of us (RIS) ran a continuous trapping program in Wongabel to determine species diversity (not frequency) from mid-1983 to mid-1984 using unbaited flight interception traps (FITs) (Peck & Davies 1980). During that period 18 species of Scarabaeinae were taken, indicating that a diverse scarabaeine fauna was present.

During a casual two-hour survey on the night of 26 December 1988, ATH found, with the aid of a headlight, 192 specimens of five species of scarabaeines sitting on leaves. Because of their abundance, we decided it was feasible to conduct a study by recording the approximate height above ground for each percher.

The perching fauna was sampled between 1900 and 2100 on the nights of 7, 16, and 21 January 1989. Sunset was approximately 1830 or earlier, with light rain in the evenings of the 16th and 21st. On each occasion headlights were used to search the vegetation along 300 m of track from ground level to eye level of the shortest surveyor—150 cm. The height above ground of each specimen was categorized against a doweling rod marked off in 15 cm increments from 0 to 120 cm. All measuring was done by the same person (ATH). Specimens were put into killing vials labelled according to the height of capture. Each beetle was later identified, and its length recorded to the nearest 0.5 mm by RIS.

Concurrent with each sampling period, a 15 watt ultraviolet light was operated in the study area to attract species that were actively flying. Insects were collected from a sheet beneath the light.

A nocturnal dung trap survey was conducted on 16 January concurrently with the perching sample. Six traps were set along one of the tracks sampled. Each trap consisted of a 200 ml transparent plastic cup baited with 5 cc of human feces on the end of a flat wooden stick, as described by Peck and Howden (1984). The contents of the cups were collected into alcohol at the end of the evening's perching survey.

On 30 January 1989 between 1700 and 2200 in the same area, we operated six traps baited with a mixture of fermenting fruits and three traps baited with commercial mushrooms in early stages of decay.

Between 24 December 1988 and 8 February 1989, two of us (HFH and ATH) spent a total of 20 hours on four different sunny afternoons in January 1989, walking the trails and tracks searching for scarabaeines either perching or associated with dung.

VOUCHERS.—Specimens from this study are deposited in the collections of the Department of Primary Industries, Mareeba, and in the H. and A. Howden Collection, Ottawa.

DATA ANALYSES OF NOCTURNAL PERCHERS.—Only one specimen of *O. bornemisszanus* was captured, so it was omitted from subsequent data analysis. The other five perching species were analyzed with a one-way analysis of variance for height of perching and length of beetle. Pairwise comparisons of species means were performed by the least significant difference procedure. Simple correlations between height of perching and length of beetle were performed for each of the three most common species, *O. dicranocerus*, *O. gulmarri*, and *T. aeneopiceum*.

RESULTS

The 1983–84 survey of RIS obtained 18 species of scarabaeines in Wongabel, and our 1988–89 study added four more. Table 1 lists the species and author, the size range of each species, and the method of collection. Additionally, *Onthophagus gazella* (Fab.), an imported African species, was taken at light, but it has not been included in the study (it was not common at Wongabel).

The nocturnal surveys yielded a total of 753 perching individuals of six species. The beetles perched almost exclusively on smooth, shiny leaves, especially those of *Ixora* sp. and, less frequently, on those of aroids. Perchers were found very infrequently on the hairy or spiny leaves of stinging nettle and rattan. It seemed to make little or no difference if the leaves were wet or dry; just as many perchers were evident on rainy nights (16th and 21st) as on

TABLE 1. *Scarabaeinae recorded from Wongabel State Forest, Queensland. Measurements for other than perching scarabs are from Matthews 1972, 1974, 1976. Subscripts of X = number collected.*

		Collecting method				
	Size (mm)	FIT	Light	Dung traps	Perching	Other
Scarabaeini						
Amphistomus calcaratus (Macleay)	6.0–8.0	X		X_6		
Amphistomus complanatus Matthews	5.5–8.0			X_1		
Boletoscapter cornutus (Macleay)	6.0–8.0	X				
Lepanus globulus (Macleay)	3.6–5.2	X		X_1		
Lepanus nitidus Matthews	3.6–4.5	X				
Monoplistes curvipes Lea	5.5–6.5	X		X_2	X_9	Beating clumps of dead leaves in daytime
Temnoplectron aeneopiceum Matthews	4.0–6.0	X	X	X_{29}	X_{132}	Fungus trap
Temnoplectron bornemisszai Matthews	11.5–12.0	X		X_{24}		
Temnoplectron politulum Macleay	5.5–6.8	X		X_1	X_{34}	
Onthophagini						
Onthophagus bornemisszanus Matthews	9.5–12.0				X_1	
Onthophagus capelliformis Gillet	9.0–12.0		X			
Onthophagus darlingtoni Matthews	8.1–8.8	X		X_1		Marsupial dung
Onthophagus dicranocerus Gillet	7.8–11.5	X	X	X_3	X_{103}	
Onthophagus gulmarri Matthews	4.4–7.0				X_{282}	Marsupial dung
Onthophagus mulgravei Paulian	5.0–6.0	X				
Onthophagus pillara Matthews	5.0–7.0	X				
Onthophagus rubicundulus Macleay	4.0–7.0	X				
Onthophagus waminda Matthews	3.4–3.9	X		X_2		Marsupial dung
Onthophagus wilgi Matthews	3.4–3.8	X		X_1		
Onthophagus yungaburra Matthews	3.5–5.5	X			X_1 1400 hr	Marsupial dung
Coprini						
Coptodactyla depressa Paulian	11.0–15.5	X	X	X_{26}		Fruit traps
Demarziella interrupta (Carter)	3.5–4.1		X			

dry nights. During the three nights when perching heights were recorded, 561 specimens were obtained; these are listed in Table 2 together with the numbers perching at each height interval for each species.

The six dung traps operated on the night of 16 January yielded 97 specimens of 12 species of Scarabaeinae (Table 1) and two species of Hybosorinae, *Liparochrus hackeri* Blackburn and *Phaeochrous emarginatus* Castelnau. Three of the scara-

TABLE 2. *Perching height and numbers of individuals.*

Species	Height in centimeters 15	30	45	60	75	90	105	120	No. collected each species
Onthophagus dicranocerus	1	20	40	24	13	4	1	—	103
Onthophagus bornemisszanus	—	—	—	1	—	—	—	—	1
Onthophagus gulmarri	6	105	115	41	12	3	—	—	282
Temnoplectron aeneopiceum	23	83	24	2	—	—	—	—	132
Temnoplectron politulum	5	24	5	—	—	—	—	—	34
Monoplistes curvipes	—	1	2	2	—	3	—	1	9
Total number	35	233	186	70	25	10	1	1	561

baeines in the traps, *Temnoplectron bornemisszai, T. aeneopiceum,* and *Coptodactyla depressa,* were each represented by more than 20 specimens. Of these three species, the relatively small *T. aeneopiceum* (4–6 mm) was found perching, while the larger *T. bornemisszai* (11.5–12) and *C. depressa* (11.0–15.5) were not. The most frequently encountered beetle in Wongabel was not a scarabaeine but *L. hackeri* (length 10.0–14.0 mm). Thirty-five specimens were taken in the dung traps. It was also taken in all other types of traps and was by far the commonest species at light but was not found perching.

The six fermenting fruit traps yielded four specimens of *Coptodactyla depressa* and 70 of *Liparochrus hackeri*. The three mushroom traps yielded one *Temnoplectron aenopiceum* specimen and four specimens of *L. hackeri.*

In the 20-hour, four-afternoon daytime survey only a single specimen, *Onthophagus yungaburra,* was found perching. Four scarabaeine species, *Onthophagus darlingtoni, O. gulmarri, O. yungaburra,* and *O. waminda* (one or two specimens each), were found in fresh possum dung (probably from one of the common ringtail possums (*Pseudocheirus* sp.).

Statistical analysis of the perching data (Table 3) shows that some species can be separated by size; for example, *O. gulmarri* from *O. dicranocerus.* Other species may perch at different heights. However, correlations between perching height and beetle length were low and inconsistent both within and among species. Larger specimens of *O. dicranocerus* tended to perch higher ($r = 0.40$, $P < 0.01$), but all sizes of *O. gulmarri* were found at all heights ($r = 0.09$, $P > 0.05$). Figure 1 graphically illustrates

TABLE 3. *Statistics on (A) height of perching (in cm) and (B) length of beetle (in mm).*

Species	No.	Mean+	s	95% C.I.	Range
(A) Height of perching					
M. curvipes	9	70.0	29.0	(61.0, 79.0)	30–120
O. dicranocerus	103	51.4	17.1	(48.7, 54.1)	15–105
O. gulmarri	282	42.7	13.8	(41.1, 44.3)	15–90
T. aeneopiceum	132	30.6a	9.7	(28.3, 32.9)	15–60
T. politulum	34	30.0a	8.3	(25.4, 34.6)	15–45
SD		13.75			
(B) Length of beetle					
M. curvipes	9	5.9a,b	0.30	(5.59, 6.29)	5.5–6.5
O. dicranocerus	103	9.6	0.87	(9.57, 9.67)	8.0–11.5
O. gulmarri	282	5.7a	0.46	(5.63, 5.75)	4.5–7.0
T. aeneopiceum	132	5.3	0.30	(5.21, 5.39)	4.0–6.0
T. politulum	34	6.3b	0.39	(6.11, 6.47)	5.5–7.0
SD		0.5			

s = standard deviation for individual sample; SD = pooled standard deviation for calculation of confidence intervals; pairs of means followed by the same letter do not differ at the 0.05 level of significance. All other pairs of means differ at the 0.01 level of significance.

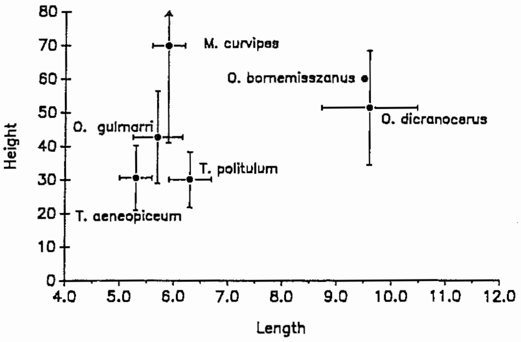

FIGURE 1. Relationship between species, height of perching and length of beetles; bar = s (standard deviation for individual sample).

the overlap in size and perching height for the species.

DISCUSSION

This study shows that some tropical Australian dung beetles commonly perch after dark. In examining the data for the height of perching in relation to the size of the beetle, it is obvious that the species studied do not stratify their perching height to the degree found for the New World tropics. The five common perching species (Table 2) perched, on average, below the 60 cm level, and all of them averaged under 10 mm in length. This is also true for most of the common perchers in the New World, particularly those of the genus *Canthidium*. A few New World species, especially those feeding on monkey dung, may perch at higher levels and are usually diurnal (Gill, in press).

While perching height does not show distinct stratification according to size, there are some generic differences. Among the Wongabel perchers there is some indication (see Fig. 1) that the perchers of the genus *Onthophagus* generally occupy a higher level than do those of the genus *Temnoplectron*, but there is a large overlap (Fig. 1).

From our baited traps and light data (Table 1), *Temnoplectron* perchers appear to be more general feeders than do the higher perching *Onthophagus*. Dung of any type was rarely seen in Wongabel. However, in our daytime searching we found four marsupial pellets that had been partly buried by *Onthophagus*. Four species were taken off the dung. Two of the species collected, *O. darlingtoni* and *O. waminda*, also were taken in baited traps but were not found perching. The single daytime percher, the rare *O. yungaburra*, was one of the two species found only on marsupial dung. The last species, *O. gulmarri*, was found on marsupial dung and was not collected in any type of trap, yet it was the most common percher. Thus two species of perching *Onthophagus* seem to prefer marsupial dung and all *Onthophagus* species that perched were mostly at levels above the smaller *Temnoplectron*.

Resource size.—The difference in average perching height may be somewhat influenced by resource size as was noted for Panamanian species (Peck and Howden 1984). The amount of human feces used in our Wongabel dung traps measured approximately 5 ± 2 cc. The marsupial pellets found were about twice the size of the feces bait. The exact size of the pellets could not be measured because they had been partly consumed by the *Onthophagus*. However, there is no doubt that the pellets were distinctly larger than the amount of feces used for the dung traps, and there is the implication that smaller, lower-sitting *Temnoplectron* favored the smaller resource while the higher perching *Onthophagus* favored the larger resource. For *O. gulmarri*, and possibly for *O. yungaburra*, there is the added implication that foraging for a particular food (marsupial dung) may be more efficient from a perch. Conversely, eight species of scarabaeine (plus the two hybosorines) taken in the nighttime dung traps were never seen to perch. Some of these may have been foraging by flying, particularly the large (10–14 mm) *L. hackeri* which was frequently taken at our light trap. Parallels for each of the above types of behavior occur in the New World tropics, but the diversity of perchers is less in Australia and the stratification is less well defined.

Resource availability.—Differences in the behavior of the Australian and New World dung beetles may be explained possibly by differences in resource availability and possibly by their evolutionary history. One obvious difference between the scarabaeines of Wongabel and those of Panama is in their size. Those from Wongabel (22 species) measure from 3.5 to 15.5 mm in length and those from Panama (28 species) measure from 3.0 to 25.0 mm. The percentage of perching species (21–22%) and their size range (3–9 mm) is approximately the same for each fauna. We suspect that the size of a species of dung beetle is influenced by the variation in the size of available dung deposits. In Panama, the larger dung beetles frequently use large deposits including those of horses or cows. According to

Janzen and Martin (1982), large-sized dung deposits from large-sized mammals have historically been present long enough in the New World tropics to allow the larger scarabaeines to develop methods for their utilization. On the other hand, a source of large dung deposits probably has not been continuously available in Australia. Even large marsupials have relatively small dung pellets, and they usually leave their dung pellets individually scattered. Few Australian species of dung beetles utilize cow or horse dung, and much of the dung beetle activity is nocturnal, as is much of the activity of the native mammal fauna. Hence it appears that resource size has historically limited species size. Both the more uniform resource size plus lower species numbers may lessen the degree of behavioral diversity, so that separation of perching heights lack the exactitude found in the New World.

EVOLUTIONARY TIME.—Evolutionary time may be a factor in another way as well. The genera of Australian perchers may be divided into two groups. The genera *Temnoplectron* and *Monoplistes* belong to relatively old Australian lineages with no species shared with other continents, but some relationships above the generic level are shared with southeast Asian and with South American beetles (Matthews 1974, p. 8). As for the origin of the Australian *Onthophagus,* Matthews (1972) hypothesizes a number of invasions (34), probably coming from southeast Asia in the Tertiary or Pleistocene, with the origin of the genus being Africa. Whatever the times of the invasions, the species of perchers at Wongabel have had to shift their food preference from dung of other mammals to marsupial dung.

This change in food, plus a possible shift in activity from diurnal to nocturnal makes us suspect that the perching habit of Australian beetles may have evolved independently from that of the New World beetles. This may also contribute to the differences noted between the New World and Australian perchers.

In considering all of our evidence, we can conclude that perching is a common habit for a limited number of scarab species occurring in rainforests of northeastern Australia. We also believe that perching, at least for some of the species (*O. gulmarri* in particular), is a type of foraging strategy. No other explanation that has been suggested for the behavior of scarab perching explains our data more adequately.

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