

## The ecology and behaviour of arboreal dung beetles in Borneo

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### ABSTRACT

Dung beetles foraging in the rainforest canopy have been recorded on every sub-continent. Work at the Danum Valley Field Centre in Sabah, Malaysian Borneo, revealed a guild of arboreal dung beetles found only metres above the forest floor up to the high forest canopy, and that feed on primate dung caught on canopy vegetation. The flight activity, spatial distribution and feeding ecology of this previously unrecorded guild of arboreal beetles is examined, and related to the ecology, behaviour and gut morphology of the primate species resident in the same forest.

The dung-relocation behaviour of the Bornean dung beetles is atypical for the genus in which they are found, and breaks with the existing dichotomy of dung beetle tribes into dung rollers and non-dung rollers. The implications of this discovery are discussed.

This work gives a very real indication of how new light can be shed on the ecology of tropical insect communities by studying the strato-orientation of insects in response to conditions in the rainforest canopy, and the importance of canopy work in forming comprehensive descriptions of rainforest arthropod communities.

### INTRODUCTION

The distribution of insects in different strata of architecturally rich habitats is a little-studied area of ecology (Sutton and Hudson, 1980; Roubik, 1993; Peng *et al.*, 1992), with most work concentrating on uniform agricultural systems in temperate latitudes (Peng *et al.*, 1992). Few studies have looked at the distribution of insects in relation to the strata of a tropical rainforest (Sutton and Hudson, 1980; Sutton, 1983, 1989). The rainforest canopy is now known to be a major source of arthropod



diversity (Erwin and Scott, 1980; Stork, 1988, 1993), and many of the species found here do not exist in any other habitat. The forest floor and the upper canopy represent two ends of a microclimatic spectrum: a transition from low-light regimes to conditions of high incident solar radiation. Selection pressures on insect populations lie between these extremes, and provide a vertical axis along which potentially competing species can differentiate spatially (i.e. 'strato-orientation', *sensu* Roubik, 1993, can occur). The canopy also provides a third dimension in which species can partition resources, in addition to the two represented by the ground surface. Given this potential for strato-orientation in tropical rainforests, such patterns may play a role in the processes that underlie and maintain regional species diversity, and enhance the spatial and temporal complexity of insect communities in such ecosystems.

In this paper, we examine the ecology and behaviour of a previously unrecorded guild of arboreal dung beetle from Borneo, and the role of strato-orientation in structuring these communities, and those of arboreal mammals on whose dung they feed. We also review for the first time the available literature on arboreal dung beetles, and show how the Bornean arboreal beetles diverge from the classic taxonomic distinction of the Scarabaeid dung beetles into dung-rolling and tunnelling species, thereby highlighting the importance of canopy work in forming complete descriptions of rainforest arthropod communities.

#### ARBOREAL DUNG BEETLES

Most species of dung beetle (family Scarabaeidae) forage within close proximity to the ground. For communities that live in open habitats, resources can only be found in two dimensions, and so ground-based foraging behaviour is the sole option available to them. Utilization of a third dimension only becomes possible when dung and carrion are available in the arboreal environment in sufficient quantities to enable any arboreal species to remain reproductively viable. In tropical rainforests, a significant portion of the vertebrate fauna is arboreal (MacKinnon, 1972; Malcolm, 1997, Chapter 25, this volume). A large proportion of the dung produced by these animals never reaches the forest floor (A.J. Davis, personal observation) as much of it is caught on branches and leaves on the way down. This paper concerns those dung beetles that forage in dung caught in the upper forest canopy and lower vegetational layers.

Dung beetles foraging in the rainforest canopy have been recorded on every sub-continent. Globally, the average ( $\pm$  S.E.) number of dung beetle species recorded from rainforest sites is  $57.9 \pm 7.041$  (based on data from 11 studies; Davis, 1993). In North Sulawesi, at least two arboreal species from a total of 46 dung and carrion beetles species recorded (Hanski and Krikken, 1991) were collected on the Royal Entomological Society of

London expedition to the Dumoga-Bone National Park in 1985 ('Project Wallace'). One of these species, *Onthophagus magnipygus* Boucomont, was rarely caught in ground traps, but regularly caught in traps at 5–20 m above the ground. The second species, *Phaeochrous emarginatus* Castelnau, a carrion specialist, was found to be active at all levels from the ground to the upper canopy (Hanski and Krikken, 1991). *O. magnipygus* may well be an arboreal specialist, whereas *P. emarginatus* is ubiquitous throughout the forest. Several canopy-feeding species have been recorded in the Neotropics. Two South American species – *Canthon angustatus* Harold and *C. subhyalinus* Harold – were observed on leaves making and rolling balls from howler monkey dung, and then falling to earth with dung balls tucked between their hind legs (Howden and Young, 1981). Other South American beetles, belonging to the genera *Trichillum* Harold, *Pedardium* Harold and *Uroxys* Westwood, live in the fur of sloths, and some species of the genus *Glaphyrocathion* Martínez likewise live on monkeys and tapirs (Halfpter and Matthews, 1966; Howden and Young, 1981). The greatest number of arboreal dung beetle species to be recorded from one site were collected in the Makokou Reserve, Gabon, West Africa (Walter, 1984), where collections comprised four species of the genus *Onthophagus* (*O. laeviceps* d'Orbigny, *O. ahenomicans* d'Orbigny, *O. possoi* Walter and *O. mpassa* Walter) and one species of the genus *Sisyphus* (*S. arboreus* Walter). Only *S. arboreus* showed ball-rolling behaviour, but was not observed on the forest floor and was presumed to exist entirely in the forest canopy. Collections from Madagascar have only revealed one arboreal dung beetle species to date: *Arachnodes goudoti* Castelnau. This small canthonine roller was found to be common in traps set in small trees, as low as 50 cm above the ground (Vadon, 1947), and was observed demonstrating the same behaviour as the South American dung rollers (*C. angustatus* and *C. subhyalinus*).

#### MATERIALS AND METHODS

Research was carried out at the Danum Valley Field Centre, Sabah, Malaysian Borneo (5°01'N, 117°47'E). Investigation of the existence of arboreal dung beetles, and if present, of their species composition, was approached by trapping and direct observation. Traps were positioned within the Danum Valley Conservation Area and in the surrounding forest within the Ulu Segama Reserve, complementing a programme of ground pitfall trapping in the area (Davis, 1993; see also Holloway *et al.*, 1992). Traps were suspended under trees within a variety of forested areas (Davis, 1993). Much of the Danum Valley Conservation Area is composed of lowland, evergreen dipterocarp forest (<760 m above sea level), where the Dipterocarpaceae make up approximately 88% of the total volume of large trees (Newbery *et al.*, 1992). Arboreal traps were of the same basic design as pitfall traps used to collect beetles from the forest floor



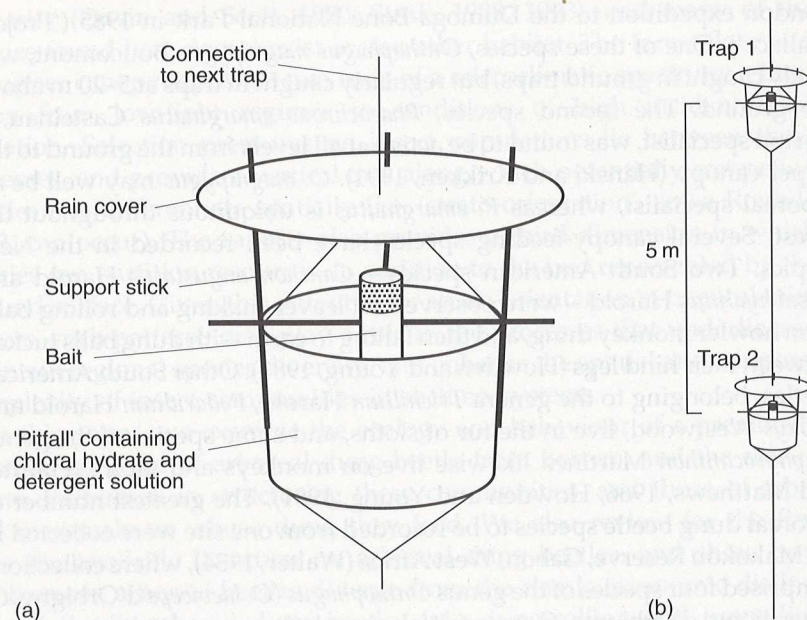


Figure 19.1 (a) An aerial 'pitfall' trap. (b) Diagram illustrating the arrangement of traps placed vertically from a tree platform. Eight aerial traps were used from 5 to 40 m in height, placed at 5-m intervals.

(Hammond, 1990; Davis, 1993), but with certain modifications. Plastic containers (12 cm diameter  $\times$  13 cm depth) were suspended by string and attached to longer pieces of rope. A plastic plate was held over the container by three sticks, to keep rain from entering the trap. The bait was held in a plastic tube, aerated at the top end, and suspended over the pitfall (Figure 19.1). Traps were baited between 08:00 h and 10:00 h, and collected 72 hours later. Pitfalls from the main collecting programme were placed at 5 m or 10 m above ground. Studies of the community ecology of dung beetle populations in Western Africa used similar 'aerial pitfall traps' (Walter, 1984), but pitfalls had platforms attached to their rim, to enable beetles to alight on a surface before approaching the bait. Initial tests at Danum Valley showed that such modifications were not necessary for this study (see below).

In addition to their use within the main pitfall trapping programme, a series of traps were set up from a canopy platform on the Danum Valley Nature Trail (an area of primary forest), along a single vertical transect. The platform was positioned on a tree that formed part of the upper canopy, adjacent to a mature strangling fig. The understorey (5–15 m in height) formed a separate vegetational layer beneath the

upper canopy. Eight aerial pitfall traps were positioned at intervals of 5 m, joined together by rope, to a height of 40 m (Figure 19.1). The transect included one pitfall on the forest floor, and was baited four times (three times with human faeces and once with carrion).

#### A NEW ARBOREAL FAUNA

Two aerial pitfall traps were hung from an observation tower on the Nature Trail at Danum Valley between 21st and 24th August, 1990 (at 5 m and 10 m), during a preliminary study on the existence, or absence, of an arboreal dung beetle fauna. This was the first time that such traps had been used in Borneo. After 72 hours the traps were emptied, and the contents examined. Remarkably, of a total 2378 beetles present in these samples (780 at 10 m and 1598 at 5 m), only one specimen (*Onthophagus pavidus* Harold) was recognized as representing a species present in collections made from ground traps in primary forest. Subsequent collections made from aerial traps within the main pitfall trapping programme also showed that, while the arboreal species were dominant in arboreal traps, they were scarce or entirely absent in ground traps (Davis, 1993). To find such high numbers of beetles so close to the ground, and yet of such a different nature to that of the ground fauna, implies that the species present in aerial traps were arboreal in habit, foraging in the upper canopy and understorey rather than the ground. Subsequent behavioural studies confirmed this hypothesis (see below).

#### Taxonomy of the arboreal fauna

The classification of dung beetles used in this paper follows Balthasar (1963) and Hanski and Cambefort (1991). A paper fully describing the taxonomy of the group is currently in preparation (J. Krikken and J. Huijbregts, in preparation).

The arboreal beetles belong to the genus *Onthophagus* Latreille, tribe Onthophagini, a genus that is abundant on the forest floor. On average, they are smaller than equivalent ground-dwelling species (being only ca. 4–5 mm in length, compared with 6–8 mm for the ground fauna). Individuals can be split into two distinct morphological groups. The first (Arboreal #1) has an elongate curved hind metatarsus, and the second (Arboreal #2), a tibial spur on the back legs (see Davis, 1993). Subsequent analysis showed that the Arboreal #2 group consists of only one species, *Onthophagus* sp.2. Arboreal #1 is dominated by one species closely related to *O. deliensis* Lansberge, 1885, although a second species has been found in small numbers (closely related to *O. falcatus* Boucomont, 1914). The taxonomy of the arboreal species is currently under revision, and will be dealt with in a future paper (see also Davis, 1993).



A third arboreal group (Arboreal #3) was found in very low numbers. This third group is represented by only one species, *Onthophagus* sp.3 (J. Krikken and J. Huijbregts, in preparation). Most were collected from one site within primary forest (11 of the 16 individuals), which suggests that this species is highly clumped. Although *Onthophagus* sp.3 shows a propensity towards foraging higher than most ground-dwelling species (56% of all specimens were collected in aerial traps), it cannot be said to be an arboreal species in the same way that *Onthophagus* sp.2 and *O. deliensis* complex (and related forms) are.

The reasons for Arboreal #1 and Arboreal #2 (*Onthophagus* sp.2) forms meriting the distinction of being truly arboreal in habit, and their position within the superfamily Scarabaeoidea, both in taxonomic and functional terms, are examined below.

#### Dung beetle functional groups

Dung beetles can be divided into four functional groups: tunnellers, rollers, dwellers, and kleptoparasites (Halffter and Matthews, 1966; Hammond, 1976; Klemperer, 1983). The ball rollers and tunnellers form the dominant functional groups in tropical latitudes, comprising the family Scarabaeidae. The Scarabaeidae is split into two subfamilies, the Scarabaeinae, which comprise the functional group of ball rollers, and the Coprinae, which are tunnellers (Table 19.1). The division of the Scarabaeidae into the Scarabaeinae and the Coprinae is seen as reflecting fundamental behavioural and taxonomic differences between species that roll balls of dung and those that relocate dung by tunnelling beneath into the soil.

**Table 19.1** The division of the Family Scarabaeidae into subfamilies and tribes. (After Balthasar, 1963.)

Subfamily	Tribe
Coprinae (tunnellers)	Coprini
	Dichotomiini
	Oniticellini
	Onitini
	Onthophagini
Scarabaeinae (ball-rollers)	Phanaeini
	Canthonini
	Eucraniini
	Eurysternini
	Gymnopleurini
	Scarabaeini
	Sisyphini

#### ECOLOGY AND BEHAVIOUR OF THE ARBOREAL BEETLES

##### Feeding specializations

No arboreal beetles were attracted to traps baited with carrion. Neither were they attracted to bat guano or common palm civet (*Paradoxurus hermaphroditus*) dung. This, along with the observation that both Arboreal #1 and Arboreal #2 are diurnal (as are the South American arboreal species), suggests that these beetles specialize in the dung of frugivores and folivores, and specifically on the dung of monkeys and apes. This hypothesis is supported by the fact that beetles belonging to Arboreal #1 were collected from freshly deposited orang-utan (*Pongo pygmaeus*) dung within the Danum Valley Conservation Area, and were also collected from orang-utan dung from within the Sepilok Forest Reserve (near Sandakan, in eastern Sabah).

##### Diel flight activity

Data on the diel flight activity patterns were obtained by trapping at regular intervals during the day and night. Five such activity studies were carried out, each over a 34-hour period. Traps were emptied at 2-hourly intervals during the day and 4-hourly intervals at night. One aerial trap was used for this purpose, located on the Nature Trail close to the Danum Valley Field Centre. Similar activity studies were also carried out on the ground fauna (Davis, 1993).

Figure 19.2 shows the flight activity of the two groups of arboreal beetles, Arboreal #1 and Arboreal #2. Figures given are average numbers of beetle per pitfall ( $\pm$  S.E). Hours of darkness were between 18:30 h and 05:00 h. Arboreal species #2 shows peak activity at dawn and dusk, with no activity towards mid-day, whereas Arboreal species #1 peaks between 12:00 h and 14:00 h. Neither group is active at night. These findings correspond with direct behavioural observations (below).

In terms of arboreal dung beetle activity, diurnal primate incidence and abundance, and in particular the time of dung deposition, can be expected to play a major role, for reasons outlined above (see also Davis, 1993). All 10 species of primate found in eastern Sabah are found in the conservation area, including the orang-utan and proboscis monkey (*Nasalis larvatus*). Several of these species are seen on a regular basis, most notably the Bornean gibbon (*Hylobates muelleri*), the red langur (*Presbytis rubicunda*), and two species of macaque (the long-tailed macaque, *Macaca fascicularis*, and the pig-tailed macaque, *Macaca nemestrina*) (A.J. Davis, personal observation).

The old-world monkeys of the subfamily Colobinae (which include the leaf monkeys, or langurs, of south-east Asia) differ from other primates