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Canopy Ferns in Lowland Dipterocarp Forest Support a Prolific Abundance of Ants, Termites, and Other Invertebrates[1]

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ABSTRACT

The epiphytic Bird's Nest Fern (*Asplenium nidus* complex) has a large basket-shaped rosette that accumulates leaf litter. We investigated the role of these ferns in supporting invertebrate populations in the primary lowland dipterocarp forest of Danum Valley, Sabah, Malaysia. Ferns were divided into three size classes: large (rosette diameter >60 cm), intermediate (30–60 cm), and small (<30 cm). Seven hectares of forest were surveyed: the canopy had a mean density of 30 large ferns/ha and 20 intermediate ferns/ha. Six large and five intermediate ferns were removed from the crowns of *Parashorea tomentella* (Dipterocarpaceae) at heights between 39 and 52 m. The largest ferns had fresh weights of *ca* 200 kg. The mean animal abundance in large and intermediate ferns was 41,000 and 8000, respectively. Termites and ants represented at least 90 percent of the abundance in these ferns. Of the 11 ferns, 4 contained a nest of *Hospitalitermes rufus* (Nasutitermitinae), while another contained a nest of an undescribed species of *Hospitalitermes*. An additional 56 small ferns were removed from the low canopy (2–6 m above the forest floor), of which only 1 contained a termite nest (*Nasutitermes neoparvus*). These results suggest that Bird's Nest Ferns contain *ca* 0.5 million termites/ha and contribute almost one ton (dry mass) of suspended soil and plant material/ha. Five of the trees containing large ferns were fogged immediately before the removal of the ferns. From these samples we were able to estimate the total number of animals in each tree crown. When each estimate was added to the abundance in each fern, the results suggested that a single large fern may contain from 7 to 93 percent of the total number of invertebrates in the crown. Although these results must be treated with caution because of the small sample size, they have important implications for studies of canopy invertebrates.

Key words: Asplenium nidus; *Borneo; canopy; epiphyte; fern;* Hospitalitermes; *Isoptera; Nasutitermitina; Pteridophyta.*

The lowland dipterocarp forests of Southeast Asia are the world's tallest tropical rain forests, with some trees reaching heights of 80 m or more (Whitmore 1984). Although relatively little is known about the upper strata of these forests, insecticide fogging has revealed the canopy to be rich in invertebrate species (Stork 1991, Floren & Linsenmair 1997). The temporal and spatial requirements of these invertebrates are closely linked to the canopy habitat (Mawdsley & Stork 1997, Basset *et al.* 2001), which in most rain forests includes substantial amounts of epiphytic plants (Benzing 1986, ter Steege & Cornelissen 1989, Freiberg 1996, Rudolph *et al.* 1998). Epiphytes contribute to the structure and function of the canopy (Nadkarni 1981, 1984), make up ten percent of all vascular plants (Kress 1986), and clearly provide important resources for many canopy animals (Basset 2001).

The epiphytic Bird's Nest Fern (*Asplenium nidus* complex) occurs throughout the forests of Southeast Asia (Benzing 1986, Parris 1997). The basket-shaped rosette of long fronds can trap substantial amounts of leaf litter; Bird's Nest Ferns can grow very large and reach fresh weights of up to 200 kg (see Results). The size, location, and structural complexity of these ferns make it seem likely that they provide unique refugia and a supply of nutrients and organic matter to many of the invertebrates that spend all or part of their time in the canopy. Studies in Queensland, Australia, on a similar epiphytic fern (*Asplenium australasicum*) suggest that the leaf litter within the fern may be just as rich in arthropods as the litter from the

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forest floor beneath it (Kitching *et al.* 1997, Walter *et al.* 1998); however, the density of Bird's Nest Ferns and the importance of these plants to invertebrate diversity and ecosystem processes within the canopy has never been investigated. Furthermore, the invertebrate communities associated with Bird's Nest Ferns cannot be sampled effectively using fogging techniques because almost all the animals remain inside the plant. Therefore, the only practical method of investigating these communities is to enter the canopy and sample the ferns directly.

The observations reported here are part of an investigation into the community structure of invertebrates inhabiting Bird's Nest Ferns. Those results will be published when all the species-level sorting is complete. In this paper we discuss the importance of Bird's Nest Ferns to the maintenance of canopy invertebrate populations. We focus on termites and ants because our results show that they are the two most abundant groups in the ferns. Both groups are known to be very abundant in the soil and litter of lowland tropical forests (Fittkau & Klinge 1973, Watt *et al.* 1997). Termites are the most important invertebrate decomposers in the tropics (Wood & Sands 1978, Collins 1983) and are vital to the maintenance of nitrogen and carbon cycles (Tayasu *et al.* 1997). Ants are at the ecological center of many tropical ecosystems (Wilson 1992) and may play a key role in helping to structure arboreal communities.

There has been considerable ecological research on the ground-level termite fauna of Southeast Asian forests (Abe & Matsumoto 1979, Collins 1983, Jones 1996, Eggleton *et al.* 1997, Jones & Brendell 1998, Eggleton *et al.* 1999, Jones 2000, Gathorne-Hardy *et al.* 2001), and standardized sampling methods have been established (Eggleton *et al.* 1999, Jones & Eggleton 2000). In contrast, our knowledge of the termite fauna in forest canopies is extremely limited and is based on indirect observations and casual samples of dead wood and nest material removed from tree crowns. "Drywood" termites (Kalotermitidae) such as *Glyptotermes* and *Neotermes* often nest in dead branches that are still attached to the tree, with colonies that can range in size from a few hundred individuals (Harris 1950) up to about ten thousand (Maki & Abe 1986). Several genera of Nasutitermitinae such as *Nasutitermes* and *Bulbitermes* build external carton nests on the sides of living trees and descend to forage for dead wood on the forest floor. Canopy fogging samples usually contain very few termites relative to the numbers of other groups such as ants (Stork 1991, Floren & Linsenmair 1997), but this is probably because fogging cannot sample termites that remain inside nests and branches. To date, however, there have been no reports of termites inhabiting arboreal ferns.

To understand the importance of Bird's Nest Ferns to canopy invertebrates and to termites in particular, we investigated the following: the density of ferns in the canopy; the abundance of invertebrates in ferns and in tree crowns; the proportion of canopy ferns that contain termites; whether the termites were nesting or foraging in the ferns; and whether ants limit or exclude termites from ferns.

MATERIALS AND METHODS

We worked in primary forest in the Danum Valley Conservation Area in Sabah, Borneo (4°58′N, 117°48′E; *ca* 100 m elev.) during 1998/1999. This conservation area covers 43,800 ha and is classified as lowland evergreen dipterocarp forest (Newbery *et al.* 1992). Annual average rainfall at the Danum Valley Field Centre is 2822 mm, with a mean annual temperature of 26.7°C and a mean annual relative humidity of 94.5 percent at 0800 h and 72 percent at 1400 h (Walsh 1990).

To determine the density of Bird's Nest Ferns, we surveyed seven 1 ha plots of primary forest. The survey consisted of two visual inspections of the canopy using binoculars. The first inspection was from the cown of an emergent tree in the center of each hectare plot. The *a priori* need for an accessible tree meant that plot selection could not be completely randomized. Each plot was created along a north–south axis, with parallel sides of 100 m. The second inspection involved walking along ten parallel transects (each 10 m wide) within each plot and surveying the canopy overhead. The location of every large-sized fern (maximum diameter of rosette at frond tips >60 cm) and intermediate-sized fern (rosette diameter 30–60 cm) was mapped. Small-sized ferns (rosette diameter <30 cm) were omitted from the survey because they were often too small to distinguish.

Six large and five intermediate ferns were removed from the high canopy. These ferns were all growing in trees of *Parashorea tomentella* (Sym.) Meijer (Dipterocarpaceae) and located at heights from 39 to 52 m above the ground. The fresh weight of the large ferns ranged from *ca* 170 to 200 kg, while the fresh weight of intermediate ferns ranged from *ca* 15 to 100 kg. We also sampled 56 small Bird's Nest Ferns (<2 kg fresh weight) from

TABLE 1. *Mean number (±SE) of animals in Bird's Nest Ferns (*Asplenium nidus *complex) and in crown fog samples collected from primary forest at Danum Valley, Sabah, Malaysia. Five large and 5 intermediate ferns were removed from the high canopy, and 56 small ferns were removed from the low canopy. Prior to the removal of the 5 large ferns, the host tree crowns were fogged and falling animals collected in trays covering 21 m².*

	Large ferns	Intermediate ferns	Small ferns	Crown fogs (21 m²)
Oligochaeta	19.4 ± 18.9	0.8 ± 0.4	2.0 ± 0.8	1.0 ± 0.8
Hirudinae	0.2 ± 0.2	0.3 ± 0.2	0.1 ± 0.04	0.4 ± 0.2
Gastropoda	4.8 ± 3.2	2.6 ± 1.3	2.3 ± 0.5	0.4 ± 0.4
Opiliones	9.6 ± 3.3	3.4 ± 1.4	0.2 ± 0.1	7.4 ± 3.2
Scorpiones	0.2 ± 0.2	0.0	0.1 ± 0.04	0.0
Pseudoscorpiones	4.6 ± 3.4	2.0 ± 1.1	0.02 ± 0.02	0.8 ± 0.6
Acari	363.2 ± 173.0	115.6 ± 52.8	2.8 ± 1.6	6.6 ± 1.0
Araneae	185.4 ± 77.5	18.0 ± 5.2	3.7 ± 0.4	63.0 ± 20.0
Isopoda	59.0 ± 50.6	24.2 ± 7.5	4.0 ± 0.9	1.4 ± 0.7
Diplopoda	24.2 ± 7.8	0.8 ± 0.4	4.5 ± 1.0	0.2 ± 0.2
Chilopoda	126.0 ± 60.0	12.2 ± 5.5	0.9 ± 0.2	5.2 ± 2.2
Symphyla	0.8 ± 0.8	0.0	0.0	0.0
Collembola	285.4 ± 135.5	266.8 ± 154.2	1.1 ± 0.3	40.0 ± 11.7
Thysanura	1.8 ± 1.3	0.0	0.0	0.8 ± 0.8
Orthoptera	6.8 ± 2.9	0.6 ± 0.4	0.5 ± 0.1	15.2 ± 7.0
Phasmatodea	2.2 ± 0.7	0.0	0.02 ± 0.02	2.6 ± 0.9
Dermaptera	26.6 ± 11.4	6.6 ± 5.4	0.0	4.4 ± 2.0
Isoptera	15,632.0 ± 10,374.3	5205.4 ± 5203.2	8.1 ± 7.8	55.2 ± 35.0
Blattodea	213.0 ± 80.4	17.0 ± 11.4	4.0 ± 0.6	19.8 ± 13.6
Mantodea	0.0	0.2 ± 0.2	0.0	0.4 ± 0.2
Psocoptera	60.0 ± 28.1	14.4 ± 11.7	0.0	20.6 ± 10.6
Hemiptera	95.6 ± 18.7	13.2 ± 6.0	2.4 ± 0.7	120.2 ± 57.4
Thysanoptera	8.6 ± 1.4	1.2 ± 0.4	0.04 ± 0.03	2.4 ± 1.3
Neuroptera	0.2 ± 0.2	0.0	0.02 ± 0.02	0.2 ± 0.2
Coleoptera	974.6 ± 340.2	45.8 ± 15.5	3.6 ± 0.5	239.4 ± 96.0
Diptera	513.4 ± 156.1	49.2 ± 23.1	1.7 ± 0.9	392.0 ± 113.7
Lepidoptera	13.2 ± 6.2	2.4 ± 2.4	0.2 ± 0.1	9.6 ± 3.8
Formicidae	22,231.2 ± 14,947.1	2186.2 ± 1922.2	602.4 ± 409.6	2237.8 ± 2100.5
Other Hymenoptera	223.0 ± 56.2	16.2 ± 12.3	27.7 ± 13.2	102.8 ± 39.2
MEAN TOTAL	41,085.0 ± 16,652.5	8005.0 ± 7358.4	673.9 ± 408.5	3353.0 ± 2413.4

the low canopy (*sensu* Moffett 2000) at heights of 2 to 6 m above the forest floor.

To gain access to the high canopy, we fired access lines into the tree crowns using a high-velocity crossbow (Ellwood & Foster 2001). Individual ferns were enclosed in mosquito netting to prevent loss of animals and leaf litter. Large and intermediate ferns were lowered to the ground using winches, ropes, and pulleys (Ellwood & Foster 2002) and then carried back to the field centre. Each fern was divided into living and dead fern leaves, fern core, and leaf litter from inside the rosette. The "core" is the central bulk within the rosette and consists of densely packed roots within a firm, peat-like matrix of organic matter. As the fern was being divided, any termite or ant nests were noted and confirmed by the presence of brood. The fern components were placed in separate large Winkler bags for one week, following the extraction method described by Besuchet *et al.* (1987). The Winkler method is very effective for ants and arthropods in general; however, it is less effective for termites and may underestimate abundance (Jones & Eggleton 2000). We therefore hand-sorted all material after it was removed from the Winkler bags to collect the remaining termites. The material was then placed in a solar drying room for one week, after which the dry mass was recorded.

Tree crowns containing five large ferns were precision fogged (Ellwood & Foster 2002) at 0600 h with the knockdown insecticide Pybuthrin® 33 (Aventis Environmental Science). To sample the tree crowns, collecting trays (21 × 1 m²) were placed at ground level. Animals were prevented from falling into the ferns during fogging by positioning fog trays above the ferns, and trays were suspended below to catch animals that fell from the ferns (Ellwood & Foster 2002). The few animals that fell from the ferns during fogging were added to the fern samples. Each fern was removed

TABLE 2. *Total dry mass of Bird's Nest Ferns (*Asplenium nidus *complex), litter and soil content, the abundance of termites, and the presence of nests in the ferns. A total sample of 6 large and 5 intermediate ferns from the high canopy and 56 small ferns from the low canopy were collected from primary forest at Danum Valley, Sabah, Malaysia. Only small ferns that contained termites are shown. ND = not determined.*

Fern no.	Fern size	Total dry mass (kg)	Litter and soil dry mass (kg)	Termite species	Termite nest present	Total number of termites
1	Large	ND	ND	*Hospitalitermes rufus*	Yes	ND
2	Large	25.8	23.2	*H. rufus*	Yes	23,951
3	Large	25.4	23.0	*H. rufus*	Yes	54,312
4	Large	23.1	20.2	*H. rufus*	No	30
				Hospitalitermes sp. nov.	Yes	1241
5	Large	23.0	20.5	*H. rufus*	No	28
6	Large	21.5	19.1	*H. rufus*	No	4
1	Intermediate	9.0	7.8	*H. rufus*	Yes	26,018
2	Intermediate	6.7	5.9	*H. rufus*	No	1
3	Intermediate	6.5	5.7	*H. rufus*	No	1
4	Intermediate	2.3	2.1	No termites	No	0
5	Intermediate	8.6	7.5	*H. rufus*	No	7
1	Small	0.7	0.6	*Nasutitermes neoparvus*	Yes	434
2	Small	0.3	0.3	*N. neoparvus*	No	8
3	Small	0.3	0.2	*H. rufus*	No	1
4	Small	0.4	0.4	*H. rufus*	No	2
5	Small	0.6	0.5	*Nasutitermes matangensis*	No	1
6	Small	0.3	0.3	*N. neoparvus*	No	7
7	Small	0.4	0.4	*Hospitalitermes* sp. nov.	No	1

from its tree two hours after fogging. The horizontal surface area of each fogged tree was measured at ground level to give its crown "footprint."

Climbing into the high canopy to remove Bird's Nest Ferns was technically and physically challenging. Furthermore, it took two days for a team of six people to insert the canopy access lines and secure a large fern of 200 kg, lower it to the ground, and carry it back to the field centre laboratory. Time constraints thus limited the size of our sample, and the following results are therefore tentative estimates.

RESULTS

The mean abundance of invertebrates in Bird's Nest Ferns was *ca* 41,000 in large ferns, 8000 in intermediate ferns, and 670 in small ferns (Table 1). Of the 28 invertebrate orders collected from the ferns, ants and termites were the most numerous. Together, these two groups represented at least 90 percent of the animal abundance in most of the ferns examined. The number of animals fogged from each crown (Table 1) was multiplied up to give an estimate for the entire tree crown based on the measured footprint. These estimates were then added to the number of animals in each of the large ferns collected from each of the trees to give crown abundance totals. In these five trees, the large ferns contained from 7 to 93 percent ($\bar{x}$ = 46%) of the total crown abundance.

The dry mass of ferns removed from the canopy and the number of termites they contained is given in Table 2. We collected four species of termites in the ferns, all of the subfamily Nasutitermitinae. Termites occurred in 10 of the 11 large and intermediate ferns from the high canopy, all of which were of the genus *Hospitalitermes*. Four of the 11 high canopy ferns contained a nest of *Hospitalitermes rufus* (Haviland), while another one contained a nest of an undescribed species of *Hospitalitermes*. Termites were found in only 7 of the 56 small ferns removed from the low canopy (Table 2) and this included just one nest (*Nasutitermes neoparvus* Thapa). The 6 remaining ferns contained individuals of *Nasutitermes matangensis* (Haviland), *N. neoparvus*, *H. rufus*, and the undescribed species of *Hospitalitermes*.

Five of the six ferns that contained a nest of termites also contained nests of at least one species of ant. The two largest ferns both contained large colonies of *H. rufus* and of a medium-sized species of *Camponotus* (a nest of at least 10,000 ants in each fern). Other ant species nesting in the ferns alongside the termite colonies included *Dolichoderus* sp. (a homopteran tender), *Polyrachis* sp. (*ni-*

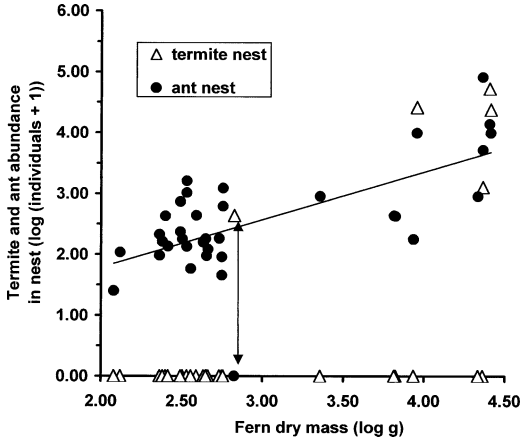

FIGURE 1. Relationship between Bird's Nest Fern (*Aspleniun nidus* complex) dry mass (log g) collected from primary forest canopy at Danum Valley, Sabah, Malaysia, and the abundance of termites (open triangles) and ants (filled circles) in nests [log (individuals + 1)] within those ferns. The regression line represents the relationship for ant nests; ant abundance = 0.785 × fern dry mass + 0.217. Symbols on the *x*-axis (abundance = 0) represent those ferns without a termite or ant nest. The arrow indicates the only small fern that contained a termite nest. This fern did not contain an ant nest.

gropilosa complex; not a termite predator), and *Pachycondyla tridentata* Smith (a predator of arthropods, including termites). Nests (*sensu* Pfeiffer & Linsenmair 1998) of the polydomous ant *Camponotus gigas* Latreille were found in four of the high-canopy ferns. This subterranean-nesting ant feeds mainly on honeydew and is known to forage in the canopy (Pfeiffer & Linsenmair 1998). Forty-two of the 56 small ferns contained an ant nest. Ant nest population size (number of individuals) was significantly correlated with fern dry mass (R^2 = 0.551, $P < 0.001$; Fig. 1).

A total of 353 large and intermediate Bird's Nest Ferns were recorded in the 7 ha of canopy, with each fern growing at least 25 m above ground level. In total, 271 trees contained one fern, 20 trees contained two ferns, 6 trees contained three ferns, and 6 trees contained four ferns. The forest canopy had a mean density of 30 large ferns/ha and 20 intermediate ferns/ha (Table 3). Using the mean number of termites in the canopy ferns (Table 2) and the mean number of ferns per hectare, we calculated that there were 479,000 (SE = 319,900) termites/ha in the large ferns and 106,000 (SE = 105,600) termites/ha in the intermediate ferns. This rough estimate indicated that there may be around 0.5 million termites/ha in the canopy ferns at Danum Valley. Furthermore, we estimated that the ferns represented a mean dry mass of 886 kg/ha (Table 3).

DISCUSSION

This study has revealed that Bird's Nest Ferns support a huge abundance of invertebrates in the high canopy at Danum Valley. Large ferns had a mean of *ca* 41,000 invertebrates, while intermediate ferns had a mean of *ca* 8000. After adding the number of animals in the large ferns to the estimated number in each of the fogged crowns, it was evident that a single large fern could contain between 7 and 93 percent of the total number of invertebrates in the crown. Of course, being based on just five large ferns in five trees, these figures must be treated with caution; however, the abundance of invertebrates in our fogging samples (mean of five trees = 160/m^2) are comparable to those recorded else-

TABLE 3. *The abundance (per ha) and estimated dry mass (kg) of large and intermediate canopy ferns in primary forest at Danum Valley, Sabah, Malaysia. Large ferns have a mean dry mass of 24 kg (SE = 0.8), and intermediate ferns have a mean dry mass of 8 kg (SE = 1.2; Table 2). The dry mass of each fern includes the organic matter and leaf litter inside the fern rosette.*

Hectare plot	Number of large ferns	Number of intermediate ferns	Large fern dry mass (kg/ha)	Intermediate fern dry mass (kg/ha)	Total fern dry mass (kg/ha)
1	33	7	792	56	848
2	24	22	576	176	752
3	27	10	648	80	728
4	16	2	384	16	400
5	35	34	840	272	1112
6	49	44	1176	352	1528
7	27	23	648	184	832
$\bar{x}$	30.1	20.3	723.4	162.3	885.7
SE	3.9	5.7	94.0	45.8	133.3

where in lowland dipterocarp forest (mean of ten trees = 117/m^2; Stork 1991), suggesting that the extrapolations give reasonable estimates. In spite of the small sample size, these figures undoubtedly have profound implications for studies of canopy biodiversity. Fogging tree crowns with large epiphytic loads may lead to very substantial underestimates of animal abundance, biomass and species richness in rain forest canopies. Bird's Nest Ferns are acting as "keystone" species by maintaining large populations of arboreal animals, and they should not be ignored in future canopy studies.

For the four termite species recorded in the Bird's Nest Ferns, this is the first documented association with canopy epiphytes. The nesting sites of *Hospitalitermes* species range from rotting tree stumps and the base of living trees (Jones & Gathorne-Hardy 1995, Miura & Matsumoto 1997) to arboreal carton nests built within and around high branches (Petch 1913, Roisin & Pasteels 1996). *Hospitalitermes* feed almost exclusively on microepiphytes such as bryophytes, algae, and lichens grazed from tree surfaces in the canopy (Collins 1979, Miura & Matsumoto 1997). This is a rare feeding habit among termites and is only known from two other genera: *Grallatotermes*, which is found in East Africa, the Philippines, and New Guinea (Roisin & Pasteels 1996) and *Constrictotermes*, which occurs in South America (Martius *et al.* 2000). *Nasutitermes neoparvus* and *N. matangensis*, which were found only in the small, low-canopy ferns, are both arboreal nesters but are most frequently observed foraging in dead wood on the forest floor. *Nasutitermes matangensis* builds large carton nests, often located 3–6 m above ground level on the sides of large living and dead trees (Jones *et al.* 1998). Previously, *N. neoparvus* has been reported building relatively smaller carton nests: one was observed *ca* 6 m above ground level, while another was found in the crown of a tall *Shorea* tree when it was felled (Jones *et al.* 1998).

It is interesting that we found no soil-feeding or litter-feeding termites in the Danum ferns. The Neotropical soil-feeding termite *Anoplotermes parvus* Snyder, which is mainly recorded from forest floor soil samples, has been found in humus inside canopy epiphytes in French Guiana (Davies *et al.* in press). The litter-feeding termite *Longipeditermes longipes* (Haviland) builds subterranean nests and forages widely across the forest floor; however, this species has also been collected from tree crowns in Sabah using insecticide fogging (Hoare & Jones 1998) and may therefore forage on leaf litter in canopy ferns. To our knowledge, the only other reports of termites associated with epiphytes are of wood-feeders. Species of *Nasutitermes* were found to be associated with bromeliads in the Caribbean (Thorne *et al.* 1996) and Mexico (Dejean *et al.* 1995).

Termite diversity on the forest floor in Danum Valley has been investigated by extensive sampling of soil, dead wood, and nests (Eggleton *et al.* 1999, Homathevi *et al.* in press). The mean density of termites on the floor of the primary forest was 1511/m^2 (SD = 565), which is equivalent to *ca* 15 million termites/ha. With the addition of the densities calculated in the present study, we can therefore estimate that *ca* 3 percent of the total known termite population in Danum Valley occurs in Bird's Nest Ferns. Other epiphytes that collect litter, such as Stag's Horn Ferns (*Platycerium* spp.), may also provide nesting sites for termites, although these ferns have not been studied. Our estimate also excludes external carton nests on trees and kalotermitids occupying dead wood in the canopy. The frequency with which kalotermitid alates are caught in light traps (Rebello & Martius 1994, Medeiros *et al.* 1999) suggests that colonies of these termites may be more abundant than previously thought. Quantitative collecting of these components of the canopy termite assemblage is still required if total species richness and abundance are to be estimated.

The only termite alates we found were in nests, confirming that colonies were mature. It is probable that the few soldier and worker termites collected in ferns without nests (Table 2) were either foraging or scouting. The smallest fern to contain a nest of *Hospitalitermes* had a dry mass of 9 kg, suggesting that there is a threshold size below which ferns are unable to support a colony of *Hospitalitermes*. This is the simplest explanation of why these nests are not found in the lower canopy, since large and intermediate ferns do not occur there. Termite and ant nests were recorded together only in large and intermediate ferns: they were never seen together in the smaller ferns (Fig. 1). Whereas 42 of the 56 small ferns contained ant nests, only 1 of the small ferns contained a nest of termites, and this fern was devoid of ants (Fig. 1). Termite nests may be uncommon in smaller ferns because the alates are unable to find enough ant-free space to avoid predation and develop a colony. Ants, on the other hand, are able to establish and maintain colonies in small ferns more successfully than termites (Fig. 1). The diversity and biomass of ants in ferns, and the coexistence of ants with other animals, will be studied in a later paper.

Bird's Nest Ferns contribute almost a ton of dry mass/ha to the canopy of Danum Valley (Table 1). The average total dry weight of canopy epiphytes reported in other forest types ranges from *ca* 1 to *ca* 14 tons/ha (Nadkarni 1984, Nadkarni & Longino 1990). With the addition of the other epiphytes that occur in the Danum canopy, the total figure is likely to be within the range for other forests types. Furthermore, Bird's Nest Ferns intercept and absorb large quantities of water. It has been shown that water accounted for 74 percent of the total fresh weight in an "average *Asplenium nidus* specimen" (Pocs 1980). This is in accordance with our own measurements of an average water content of 63 percent (SE = 2.8%) in the *A. nidus* complex (M. D. F. Ellwood, pers. obs.). Therefore, Danum Valley probably contains over 3.5 tons/ha (fresh weight) of suspended soil and plant material in the form of Bird's Nest Ferns alone.

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