

# Predation risk for herbivorous insects on tropical vegetation: A search for enemy-free space and time

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**Abstract** Spatial and temporal variability in predation risk for herbivores on 13 rainforest species of *Ficus* (Moraceae) in Papua New Guinea was studied in order to assess whether predator-free refuges exist on their foliage and if so, whether herbivorous insects concentrate their activity in such refugia. Predation risk from invertebrate predators was measured as the disappearance rate of live termites set up as baits on the foliage. By far the most important predators were ants, accounting for 77% of attacks. No consistent differences in predation rate between *Ficus* species were found so that tree identity could not be used as an indicator of enemy-free space. Predation risk was highly variable among conspecific trees and also changed rapidly in time, over periods as short as 10 days. Such short-term and unpredictable predator-free refuges may be difficult for herbivores to find and exploit. Predation risk during the day was three times higher than during the night, but abundance of herbivores on the foliage was also higher during the day. Thus, night was confirmed as a relatively enemy-free time which, however, was not exploited by herbivores.

**Key words:** ants, *Ficus*, Papua New Guinea, predators, rain forest, termite baits.

## INTRODUCTION

Several literature reviews show convincingly that predation is important in moulding the niches of arthropods and that foraging by natural enemies may prevent successful use of resources, particularly for insect herbivores (Jeffries & Lawton 1984; Bernays & Graham 1988; Berdegue *et al.* 1996). Ants are a major group of invertebrate predators in litter and on the foliage of tropical rain forests, both in terms of individuals and biomass (Wilson 1959; Leston 1978; Erwin 1983; Wilson 1987; Tobin 1991; Basset *et al.* 1992; Majer 1993; Stork & Brendell 1993). The relationships between ants, insect herbivores and plants in rain forests have been studied with particular emphasis on specialized interactions, such as those involving myrmecophilous plants (Fowler 1993; Fiala *et al.* 1994; Jolivet 1996), leaf-cutting ants (Howard 1988), or herbivores and ant species associated with acacias (Janzen 1966). However, widespread interactions between free-living insect herbivores and ants foraging on tropical foliage have received only marginal attention (but see Janzen 1972; Koptur 1984; Smiley 1985; Whalen & Mackay 1988; Letourneau *et al.* 1993). In general, foraging and predation by ants on tropical foliage resulted in a reduced

load of insect herbivores on their host plants (expressed in terms of abundance, biomass or species richness), although exceptions existed.

Since most of the literature suggests that predation in tropical rain forests represents a significant selection pressure on insect herbivores, it is important to know whether some safe 'refuges' exist, i.e., whether, for a given insect species, some locations on the foliage at any particular time show reduced risk of predation. These refuges could be located both spatially and temporally. With reference to its spatial component, predation risk may differ between (i) plant strata (e.g. understorey and canopy); (ii) plant species; and (iii) microhabitats within the plant. With reference to its temporal component, predation risk may vary with seasonal events and time of day. The information available suggests that predation by ants differs between plant strata, being higher in the canopy than in the understorey (Olson 1992). However, there may be no consistent differences in abundance and species composition of ants between various species of rainforest trees, except for those involved in ant-plant mutualism (Fiala *et al.* 1994; Floren & Linsenmair 1997). Temporal variability in predation, and particularly whether the density, activity or predation rate by ants vary with time of day, has rarely been investigated in tropical rain forests (Springate & Basset 1996).

The present study on several species of *Ficus* in a lowland forest in Papua New Guinea tests whether

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predation risk for herbivorous insects differs between plant species, between individual, conspecific trees, and between day- and night-time. Comparisons of herbivorous and predatory activity among various tree species, and between day and night, are obvious starting points in the investigation of predation-free refuges and their use, as many insect species are known to be associated with only certain tree species or are predominately either diurnal or nocturnal.

## METHODS

Our study was performed in primary and secondary lowland forests at three sites in the Madang district of Papua New Guinea: near Baitabag, Ohu and Mis Villages (145°41–8'E, 5°08–14'S, ~50–200 m). Usually, there is a distinct dry season from July to September in the Madang area and the average annual rainfall is 3588 mm; air temperature varies little during the year, with mean monthly temperature ranging from 26.2 to 26.7 °C (long-term averages for Madang from McAlpine *et al.* 1983). A general description of a forest site (Baiteta), similar to our sampling sites, is given by Bowman *et al.* (1990).

Thirteen, locally common species of *Ficus*, most of them small to medium-sized understorey trees, were selected for the study (Table 1 for species list; Basset *et al.* 1997 for further details on their biology). Predation risk on these trees was estimated by recording the disappearance of live baits from the foliage (adapted from Olson 1992). Baits consisted of workers of *Microcerotermes biroi* (Desneux) 1905, a common termite species in coconut plantations near Madang.

**Table 1.** Predation on baits exposed on the foliage of various species of *Ficus*

<i>Ficus</i> species	Median	Minimum–Maximum	<i>n</i>
<i>F. bernaysii</i> King	6	1–29	20
<i>F. botryocarpa</i> Miq.	2.5	0–18	20
<i>F. conocephalifolia</i> Ridley	4.5	0–24	20
<i>F. copiosa</i> Steud.	6	0–29	17
<i>F. dammaropsis</i> Diels	5	0–30	20
<i>F. hispidioides</i> S. Moore	7.5	0–15	14
<i>F. nodosa</i> Teysm. & Binn.	4	0–22	13
<i>F. phaeosyce</i> Laut. & K. Schum.	2	0–25	20
<i>F. pungens</i> Reinw. ex Bl.	4.5	0–15	20
<i>F. septica</i> Burm.	2	0–26	14
<i>F. trachypison</i> K. Schum.	3.5	0–28	20
<i>F. variegata</i> Bl.	5	0–23	19
<i>F. wassa</i> Roxb.	5	0–17	20

Median, minimum and maximum are numbers of baits attacked by predators per experiment. *n*, number of experiments, each representing a 30 minute exposure of 30 baits on the foliage of a single *Ficus* tree. Differences between *Ficus* species are not significant (Kruskal–Wallis test,  $P > 0.10$ ).

Each bait was secured on the upper leaf surface by an insect pin. Thirty such baits were set up on each individual tree, all within the understorey or middle canopy strata. After 30 min, the disappearance of the baits or the attendance of predators at the baits was recorded. All experiments were performed during dry weather, between 1000 and 1500 h (temperature 28–31 °C) or between 2000 and 2400 h (temperature 24–26 °C). All predators attending baits were classified to broad taxa; ants were collected and later identified by R. Snelling (Natural History Museum of Los Angeles County). Insect vouchers were deposited at the Natural History Museum of Los Angeles County, and at the Bishop Museum, Honolulu.

Two series of experiments were performed, in order to quantify differences in predation risk among various tree species and between day and night, respectively: (i) diurnal experiments on the foliage of 13 species of *Ficus*, with 13–20 replicates per tree species; (ii) diurnal and nocturnal experiments on 46 trees of *Ficus wassa*, with two experiments during the day (the second 8–13 days, usually 10 days after the first) and two experiments during the night (each 1–5 days, usually 2 days after the diurnal trials) performed on each tree. There were 22 additional diurnal experiments on *F. wassa* from which the disappearance of the baits was recorded after 30, 60, 120 and 180 min of exposure. This series of experiments evaluated the reliability of results from the 30 minute trials. Experiments were conducted between 1 April and 30 May 1996.

In April–June 1996, herbivore density on the foliage was estimated. During three visits in the day and three in the night, all externally feeding herbivores were recorded from accessible parts of the foliage of the 46 trees of *F. wassa*, used previously for predation experiments. Exactly the same foliage was searched during day and night by the same person. The leaf area searched varied among individual trees, due to their various accessibility, but the day *vs* night comparisons for each tree were based on identical sample sizes. Insect herbivore densities were also measured on another 168 trees of *F. wassa* in the same location during June–July 1998, following the same protocol. These two data sets were analysed together.

## RESULTS

Most of the predation detected on the foliage of *F. wassa* was from ants. Ants attacked 725 of the 5520 baits exposed on *F. wassa*, while all other predators combined attacked only 94 baits. Another 124 baits disappeared during the experiments, probably from predation, but it was not possible to establish the responsible predator (Table 2). Thus, the 24 species of ants found attending baits (Appendix 1) were responsible for ~77% of the total predation.

**Table 2.** Predation on baits exposed on the foliage of *Ficus wassa* during day and night

	Predators					Not attacked
	Ants	Orthoptera	Spiders	Others	Unknown	
Day	623	4	20	1	54	1356
Night	102	58	5	6	70	2519

Total number of baits attacked by ants (see Appendix 1 for species identifications), orthopterans (Gryllidae, Gryllacrididae), spiders, predators from other taxa, unknown predators and the number of baits not attacked at all during 92 day and 92 night experiments carried out on 46 trees. Number of attacks during day and night significantly departs from 1:1 ratio for ants, orthopterans, and spiders ( $\chi^2$  test,  $P < 0.05$ ).

**Table 3.** Predation on baits exposed on the foliage of *Ficus wassa* during day and night

	Predation total		Predation by ants	
	Median	Range	Median	Range
Day	16	0–49	12	0–48
Night	3	0–20	0	0–16
<i>P</i>	<0.001		<0.001	

Median and range refer to the number of baits attacked during 2 day and 2 night experiments established on each tree; 46 trees used for each comparison. Each experiment represents a 30 minute exposure of 30 baits on the foliage of a single *Ficus* tree. *P* = significance of day vs night differences, Wilcoxon signed rank test.

There were no significant differences in diurnal predation risk among 13 species of *Ficus* studied. The number of termite baits attacked was highly variable among conspecific trees, but median values for particular *Ficus* species fell within the narrow range from 2 to 7.5 baits attacked per experiment (Table 1).

Predation risk on the foliage of the *F. wassa* was much higher during day-time than during night-time (Table 3). This difference could be attributed largely to differences in the predation by ants. Predation by spiders was much less important but followed the same trend of predominantly diurnal activity, while the orthopterans were the only large group of predators more active during the night (Table 2). Most of diurnal predation resulted from three ant species *Tapinoma melanocephalum*, *Camponotus vitreus* and *Oecophylla smaragdina*. These ants were less active at night, but still accounted for a large portion of total observed nocturnal predation. Only one abundant ant species, *Crematogaster* species A, was active primarily during the night (Appendix 1).

Repeated estimates of the predation risk on the same tree, performed with a time lapse of ~10 days, were not correlated with each other either for diurnal or nocturnal predation (Spearman  $r = 0.14$  and  $0.28$  respectively,  $P > 0.05$ ,  $n = 46$ ).

However, at one time, there was a close correlation between the number of termite baits disappearing during first 30 min of the experiment and during the

following 150 min (Spearman  $r = 0.71$ ,  $P < 0.001$ ,  $n = 22$ ).

Most of the herbivores found on the foliage of *F. wassa* were species of Chrysomelidae (Eumolpinae), Curculionidae, Cicadellidae and Acrididae. There were no homopterans tended by ants on the trees used for experiments. The number of herbivores on the foliage of *F. wassa* was low, with many trees harbouring only a few insects on foliage sampled (Table 4). The total abundance of herbivorous insects on these trees was significantly higher during the day than night, but this difference was smaller in magnitude than that of predation risk (Table 4). There were marked differences between herbivorous taxa as hemipterans and beetles were more abundant during the day, whereas orthopterans were more abundant during the night (Table 4). No significant differences between day and night were found for caterpillars and stick insects, but that could be due at least in part to small sample sizes.

## DISCUSSION

### Biases of the predation risk estimates

The potential impact of predators on herbivores can be best quantified by the predation risk and mortality rate from predation, i.e. the probability of being attacked and killed by a predator during a certain period of time. The impact of predators on herbivores may be estimated accurately by experimental removal of the predators (Whalen & Mackay 1988; Dial & Roughgarden 1995) or by direct measurement of mortality rates they inflict on herbivores (Weseloh 1993; Bernays 1997), but technical difficulties usually restrict direct measurement of predation risks and rates to simple predator/prey systems, usually involving only a few species (Berdegue *et al.* 1996; Bernays 1997). These approaches are especially difficult to apply in tropical rain forests where insect herbivores are usually difficult to trace and their densities are rather low (Basset *et al.* 1992). In community studies, predation risks and rates are more often indirectly inferred, from the ratio between predator and prey densities (Warren & Gaston 1992).

**Table 4.** Abundance of various groups of herbivores on the foliage of *Ficus wassa* in day and night

	Hemiptera	Orthoptera	Phasmatodea	Coleoptera	Lepidoptera	Total
Day						
Median	2	0	0	1	0	4
25-75%	1-4	0-0	0-0	0-3	0-0	2-8
Total	598	64	24	430	60	1188
Night						
Median	1	1	0	0	0	4
25-75%	0-3	0-2	0-0	0-1	0-0	2-6
Total	446	278	20	186	44	974
<i>P</i>	<0.01	<0.001	>0.5	<0.001	>0.1	<0.05

Number of herbivores found on 214 trees of *F. wassa* in day and night. Each sample combines data from three samples, each from a different day or night. Median and the first and the third quartile for the number of herbivores on individual trees, and the total number of herbivores across all trees sampled, are given for each taxon. *P* = significance of day *vs* night differences, Wilcoxon signed rank test. Lepidoptera: only caterpillars included.

Experiments with live baits measure predation risk more directly, but use artificial situations when an immobilised, palatable and vulnerable bait is exposed to predators (Oliveira *et al.* 1987a, 1987b; Olson 1992; Weseloh 1993). The abundance and activity of ants can be estimated by distributing baits in habitats frequented by ants (Greenslade & Greenslade 1971). Such experiments can provide information on habitat use and activity patterns at a very fine scale (Bestelmeyer 1997), but other problems arise with this approach. For example, baits may only attract certain predators (Greenslade & Greenslade 1971). Problems related to bait selectivity may be overcome by using baits such as termites which are particularly palatable to many ants (Hölldobler & Wilson 1990). In such case, a low predation rate on the baits is a good indicator of an overall low predation risk.

Experiments with immobilized baits do not take into account the probability of prey escape from predators (Lima 1992), or of the prey defending themselves against predators (Dyer 1995). Conversely, herbivores may increase their exposure to predators by perambulation or feeding activity (Bernays 1997). Thus the method is poorly suited for direct measurements of absolute predation risk. However, relative differences in the rate of attacks on the baits should be correlated with the activity of predators at the sites of the baits and hence with risks of predation for *Ficus*-dwelling insect herbivores. The experiments with live baits are thus appropriate to describe relative differences in predation risks between different habitats or times.

The predation experiments using termites are especially suitable for community studies as they provide a standardized measurement of the attack rate on a palatable, immobilized prey, free from effects of idiosyncratic defence or escape responses by particular species of prey. Obviously, more realistic experiments using particular herbivores from the community under

the study would provide more accurate estimates of their individual predation risk. With at least 332 species of herbivores found on the foliage of *F. wassa* (Basset & Novotny in press), there would be thousands of individual predator-prey combinations to be tested, demonstrating the impracticability of this seemingly more rigorous approach (cf. Lawton 1991).

All conclusions from this paper are based on experiments measuring predation risk during a period of 30 mins, but these results may be extrapolated to, at least, a period of 180 mins, and perhaps longer, as demonstrated by the series of longer-term experiments.

#### Spatial and temporal variability in predation risk

By far the most important group of invertebrate predators foraging on *Ficus* trees was ants, as in virtually any tropical rain forest ecosystem. The most common ant species in our samples, *Tapinoma melanocephalum*, was active during both day and night. This species can be described as an ubiquitous tramp species (i.e. a species dispersed throughout the world by human commerce and one that lives in close association with humans, *sensu* Hölldobler & Wilson 1990). It is often found in secondary, but not primary forests (B. Fiala pers. comm. 1997), and is also a generalist ground forager (Wilson & Taylor 1967; R. Snelling pers. comm. 1997). The other common daytime foraging ant species, such as *Camponotus vitreus* and *Oecophylla smaragdina*, appear to be arboreal generalists. *Oecophylla smaragdina* is abundant and dominant over much of its geographical range (Hölldobler & Wilson 1990). The few other identified species collected at night, such as *Tetramorium insolens* and *T. validiusculum*, appear to be generalist ground foragers (R. Snelling pers. comm. 1997).

Predation rates measured on the foliage in this study were similar to Olson's (1992) measurements in the understorey of a primary forest in Cameroon (26% of baits removed). Olson suggested that the understorey could act as a microhabitat refuge for arthropods, since a far greater rate of predation was observed in the canopy, where 75% of the baits were removed. Similarly, ant density in a rain forest in Cameroon was almost 10 times greater in the canopy than in the understorey (Basset *et al.* 1992). However, herbivores were also more abundant in the canopy, presumably due to the greater resources available to them.

Our study of 13 *Ficus* species showed that tree identity cannot be used as an indicator of predation risk. This is unsurprising since the most important predators—ants—usually do not forage by plant species. For instance, ant communities studied on tropical trees by Floren and Linsenmair (1997) were very unpredictable in composition and abundance. Re-colonization of trees treated by insecticide produced quite different ant communities. Further, Basset (1995, 1996), comparing the abundance of predators and herbivores on 10 unrelated rainforest tree species, found that predator-prey ratios were relatively constant among the tree species.

Within a single tree species (*F. wassa*), predation risks were not only highly variable spatially, among individual trees, but were also variable over time, over periods as short as 10 days. Such short-term variability makes predator-free refuges difficult to exploit, particularly by less mobile herbivores or by females searching for safe oviposition sites. This variability in predation risk was particularly high during the day, due to flexibility of foraging routes by ants. Trees safe during the day often became unsafe during the night and *vice versa*, mainly as a result of the different taxonomic composition of diurnal and nocturnal predators.

In the present study, higher predation risk in the day coincided with higher density of herbivores during that period, so that although there were fewer predators at night, this was not exploited by herbivores. This supports the results by Springate and Basset (1996), who sampled rainforest arthropods by canopy flight-interception traps and found the activity of both entomophages and their potential prey higher during day than night. This result contradicts the notion that herbivore behaviour evolves in response to pressure from predators. In the absence of data on the foraging success of predators, it cannot be determined whether or not the observed pattern of herbivore abundance and predation risk reflect adaptations of predators.

Several factors may counteract the potential advantage for herbivores of escaping from predators by foraging at night (see Berdegue *et al.* 1996 for a rigorous approach to testing enemy-free space). For example, diurnal or nocturnal activity may be determined physiologically (by sensory abilities, for instance) and

may be conservative phylogenetically. Certain lineages clearly exhibit a general tendency towards either diurnal or nocturnal activity.

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**Appendix 1.** Ants attacking baits exposed on the foliage of *Ficus wassa* during day and night

Species	Day	Night
<i>Camponotus vitreus</i> (F. Smith)	23	2
<i>Camponotus</i> sp. A	0	1
<i>Camponotus</i> sp. B	1	0
<i>Crematogaster flavitarsis</i> Emery ?	3	0
<i>Crematogaster polita</i> (F. Smith)	5	1
<i>Crematogaster</i> sp. A	0	5
<i>Crematogaster</i> sp. B	2	2
<i>Crematogaster</i> sp. C	1	1
<i>Crematogaster</i> sp. D	1	1
<i>Crematogaster</i> sp. E	0	1
<i>Monomorium floricola</i> (Jerdon)	1	0
<i>Oecophylla smaragdina</i> (F.)	11	2
<i>Paratrechina vaga</i> (Forel)	0	1
<i>Paratrechina</i> n. sp. ?	0	1
<i>Paratrechina</i> sp.	0	1
<i>Tapinoma melanocephalum</i> (F.)	43	10
<i>Tapinoma</i> sp.	0	1
<i>Technomyrmex albipes</i> (F. Smith)	1	0
<i>Tetramorium insolens</i> (F. Smith)	1	2
<i>Tetramorium lanuginosum</i> Mayr	1	0
<i>Tetramorium validiusculum</i> Emery	1	1
<i>Tetramorium</i> sp.	0	1
<i>Turneria arbusta</i> Shattuck	1	0

The number of trees, out of a total of 46 tested, where at least one bait was attacked by a particular ant species is reported. Species identifications by R. Snelling.