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Predation on exposed and leaf-rolling artificial caterpillars in tropical forests of Papua New Guinea

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Abstract: Although predation is generally seen as one of the key factors determining the abundance and composition of insect herbivore communities in tropical rain forests, quantitative estimates of predation pressure in rain-forest habitats remain rare. We compared incidence of attacks of different natural enemies on semi-concealed and exposed caterpillars (Lepidoptera) in lowland and montane tropical rain forests, using plasticine models of caterpillars. We recorded attacks on caterpillars in four habitats: primary forest, secondary forest and forest fragment in lowlands (200 m asl), and montane primary forest (1700 m asl). We used 300 exposed and 300 semi-concealed caterpillars daily, and conducted the experiment for 6 d in every habitat. Daily incidence of attacks was higher on exposed caterpillars (4.95%) than on semi-concealed (leaf-rolling) caterpillars (2.99%). Attack pressure of natural enemies differed also among habitats. In the lowlands, continuous primary and secondary forests had similar daily incidence of attacks (2.39% and 2.36%) which was however lower than that found in a primary forest fragment (4.62%). This difference was caused by higher incidence of attacks by birds, ants and wasps in the forest fragment. The most important predators were birds in montane rain forests (61.9% of identified attacks), but insect predators, mostly ants, in the lowlands (58.3% of identified attacks). These results suggest that rapid decrease in the abundance of ants with altitude may be compensated by increased importance of birds as predators in montane forests. Further, it suggests that small rain-forest fragments may suffer from disproportionately high pressure from natural enemies, with potentially serious consequences for survival of their herbivorous communities.

Key Words: ants, birds, Lepidoptera, model caterpillars, parasitoids, predation pressure, primary, rain forest, secondary

INTRODUCTION

Populations of herbivorous insects are controlled by food resources (bottom-up control) and natural enemies (top-down control) (Hairston *et al.* 1960). Since the introduction of this concept, the relative importance of these two factors has received considerable attention (Lewinsohn *et al.* 2005, Richards & Coley 2007, Walker & Jones 2001).

In externally feeding caterpillars (Lepidoptera), predation is the main cause of mortality (Dempster 1983, Feeny *et al.* 1985). The pressure from natural enemies depends on forest type and the degree of disturbance, which can impact predator abundance (Barlow *et al.* 2006, Perfecto & Vandemeer 1996, Trollope *et al.* 2009, Zanette *et al.* 2000) or their ability to find prey (Philpott *et al.* 2006, Richards & Coley 2007). In particular, abrupt edges in disturbed areas are associated with higher predator (Didham *et al.* 1996, Faveri *et al.* 2008, González-Gómez *et al.* 2006, Kareiva 1987, Saab 1999, Sieving & Willson 1998) or parasite abundances (Doak 2000, but see Kruess 2003) in fragmented forests. Altitudinal trends in predation pressure are poorly known since most of the studies in the tropics have focused on the lowland forests (Novotny & Basset 2005), however, there are studies on how predators, parasitoids and prey vary with altitude (Hodkinson 1999, Rodríguez-Castañeda *et al.* 2010, 2011; Samson *et al.* 1997, Sanders 2002, Sivinski *et al.* 2000).

Caterpillars use a range of defences to protect them against attacks. Free-living caterpillars often rely on chemical protection, warning coloration or hairs (reviewed by Witz 1990). Leaf rolls, folds and ties also protect caterpillars from predators, particularly birds, ants and wasps (Atlegrim 1992, Cappuccino 1993, Loeffler 1996). However, leaf refuges can also serve as cues to predators and thus have negative effects on survival

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of their inhabitants (Nakamura & Ohgushi 2003), as demonstrated for birds (Murakami 1999, Robinson & Holmes 1982), and predatory and parasitic wasps (Gentry & Dyer 2002, Weiss *et al.* 2004).

Predation events, in contrast to parasitism or herbivory, can only be rarely observed in nature as they happen fast. The impact of predators on prey may be estimated accurately by experimental removal of predators or by direct measurement of mortality rates. The use of artificial models of prey have already proved suitable for the assessment of relative predation pressure by different predators – birds, mammals and ants – as each group leaves recognizable marks on the attacked caterpillar (Faveri *et al.* 2008, Koh & Menge 2006, Loiselle & Farji-Brener 2002, Posa *et al.* 2007, Richards & Coley 2007).

In this study, we use artificial caterpillars exposed in tropical rain forests of New Guinea to test the following hypotheses: (1) incidence of attacks will be higher on exposed than on semi-concealed caterpillars, (2) predation by ants will decrease and that by birds will increase with altitude, and (3) incidence of attacks will increase with the intensity of forest disturbance.

METHODS

We conducted our study at four tropical forest sites in Papua New Guinea: (1) Wanang 3 (5°13.5′S, 145°04.9′E, 120 m asl), situated within > 10 000 ha of contiguous lowland primary forest in the Wanang Conservation Area; (2) Wanang 1 (5°14.2′S, 145°10.9′E, 125 m asl), a mosaic of primary and secondary lowland rain forest near Wanang 1 Village situated on the border of the Wanang Conservation Area; (3) Ohu (5°16.2′S, 145°41.1′E, 170 m asl), a 300-ha fragment of lowland primary forest near Ohu Village, surrounded by secondary forest created by slash-and-burn agriculture; (4) Kotet (6°9.77′S, 146°50.37′E, 1700 m asl), a montane primary rain forest in the Finisterre Mountains close to Kotet Village.

The lowland study sites have a humid climate with a mild dry season from July to September; the average annual rainfall is 3600 mm and the annual average temperature is 26.5 °C (McAlpine *et al.* 1983). The Kotet area has a lower montane humid climate with a mild dry season from April to September. Average annual rainfall is 4000 mm (McAlpine *et al.* 1983) and average temperature 17 °C (Tvardikova & Novotny, unpubl. data).

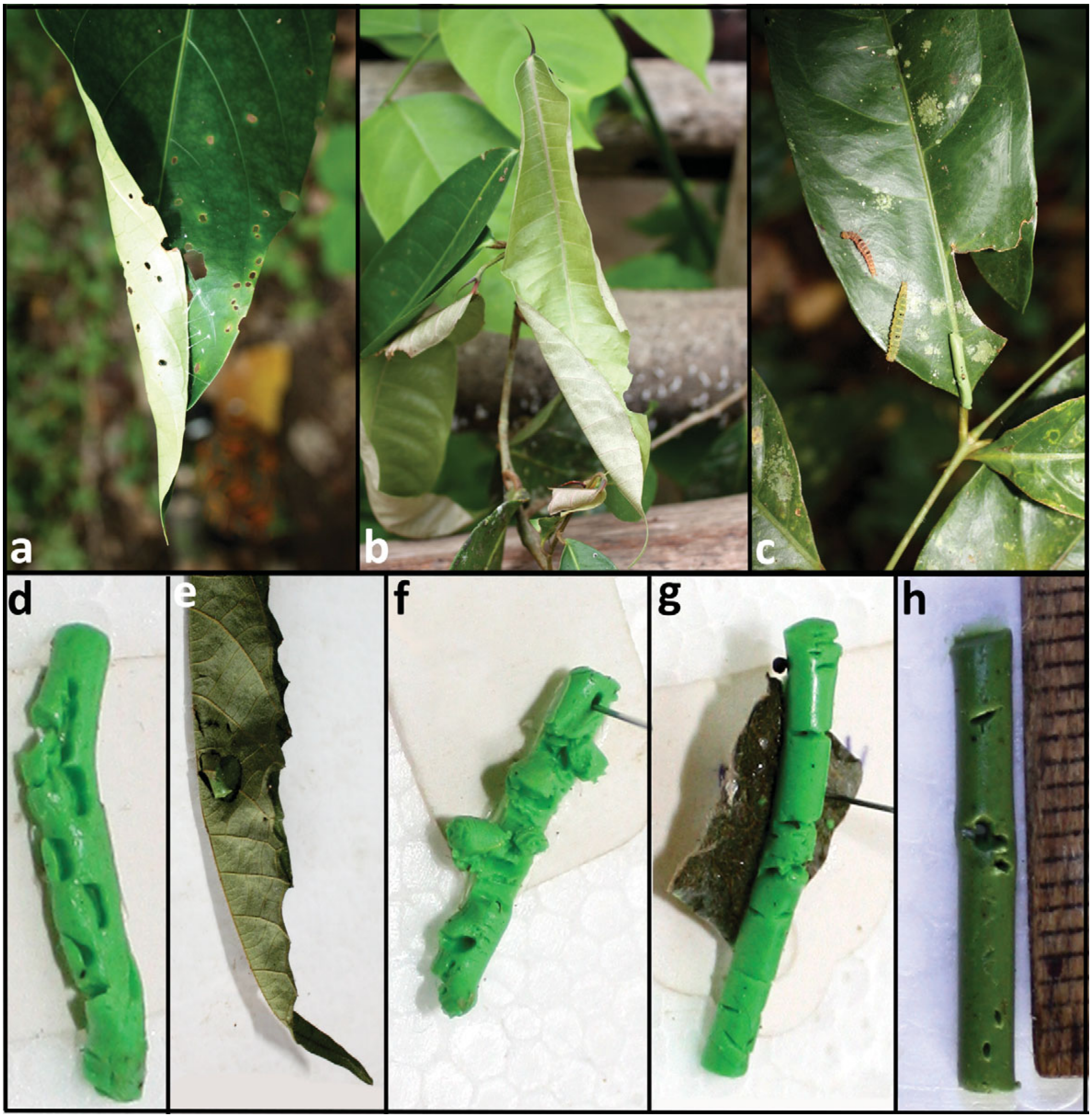
We used artificial caterpillars exposed on vegetation to monitor attack by predators and parasitoids. They were made from modelling clay (Koh-I-Noor Hardtmuth brand), which is malleable, oil-based and non-toxic. Artificial caterpillars were modelled by pressing the plasticine through a syringe. The syringe was used to ensure that each caterpillar had an absolutely smooth surface. Artificial caterpillars were 15 mm long and 3 mm in diameter, matching in body size locally common crambid and tortricid caterpillars, as well as median size in the entire caterpillar community (Novotny & Basset 1999). A mixture of brown and green modelling clay was used to create a natural-looking dark green colour. Models of free-living caterpillars resembled in size and appearance several locally common caterpillars including those from the genus *Imma* (Immidae). Leaf folds of semi-concealed caterpillars resembled natural leaf folds of *Choreutis* species. The real and artificial caterpillars and folds are shown in Figure 1.

We conducted our experiments only on selected, phylogenetically related tree species, mimicking a possible host plant range of a caterpillar species and thus its natural spatial distribution on the vegetation. In this way we also controlled for the effects of tree species between sites and habitats, including the size, shape and surface of leaves of the experimental trees. Our focal species were *Ficus congesta* Corner, *F. conocephalifolia* Ridley, *F. badiopurpurea* Diels and *F. bernaysii* King. They were selected because of their broad distribution along disturbance and altitudinal gradients; at least three of these species were common at each experimental site (*F. congesta* was rare in Ohu, and *F. bernaysii* was nearly absent in Kotet and Wanang 1 and 3). The studied forests, particularly in the lowlands, include also numerous other *Ficus* species with species-rich herbivore communities (Basset & Novotny 1999, Novotny *et al.* 2005).

Each experiment was conducted along a single 2175-m-long transect at each study site. Thirty sampling points (about 75 m apart) were established along each transect. Within a radius of 20 m from each sampling point, all suitable saplings of the four focal species (2–5 m high) were marked with flagging tape at their base. Twenty (10 exposed and 10 semi-concealed) artificial caterpillars were placed on the focal *Ficus* trees at each sampling point, between 3 and 5 m above the ground. All experiments were completed between December 2010 and March 2011.

Exposed caterpillars were pinned on the distal half of leaf so that the head of the pin was hidden in modelling clay. Artificial semi-concealed caterpillars were pinned on the basal half of a leaf and the leaf was then folded over it and fixed by a drop of Super Glue. Artificial caterpillars were at least 30 cm apart from one another. We used 10 exposed and 10 semi-concealed caterpillars per site, i.e. a total of 600 artificial caterpillars along each transect.

Each caterpillar was inspected at 24-h intervals for six consecutive days and carefully examined for characteristic bite marks (Figure 1). Missing caterpillars were excluded from the analyses as their status could not be ascertained. All missing caterpillars were replaced by new individuals. Caterpillars with some marks were collected and replaced by new caterpillars in the same



COLOUR

Figure 1. Attack marks by individual predator groups of natural enemies and semi-concealed and exposed caterpillars, and their plasticine models: leaf fold created by a real caterpillar of genus Choreutis (a), model of a leaf fold with a plasticine caterpillar hidden inside (b), a real caterpillar of genus Imma and a model of a free living caterpillar (c), bite marks by a small rodent (d), bird's beak mark on a roll of semi-concealed caterpillar (e), beak marks by a bird (f), caterpillar predated by a wasp (upper part) and by an ant (lower part) (g), bite marks by an ant (upper part) and ovipositor marks by a parasitoid (lower part) (h).

locations. Predated caterpillars were transported to the laboratory where they were examined for signs of predation or parasitism under a stereomicroscope.

Markings on the plasticine models were compared with images in the literature (Howe *et al.* 2009, Posa *et al.* 2007) and our own reference collection of plasticine models offered to common predators. Damage of uncertain origin was photographed and identified later. Detailed investigations of mandible marks on smooth surfaces aided differentiation of many potential predators, and enabled us to recognize attacks by ants of different sizes (Formicidae), birds (Aves), rodents (Rodentia), predatory wasps (Hymenoptera: Vespidae) and parasitoid wasps (Hymenoptera: Ichneumonoidae), which left ovipositor marks (Howe *et al.* 2009). Various types of marks by natural enemies are shown in Figure 1. We also tested whether predators were attracted to plasticine material by comparing attacks on 10 exposed caterpillars and 10 plasticine balls (5 mm in diameter) exposed on five trees for 24 h at every experimental site.

We estimated canopy openness from canopy photos (Canon 450D, same settings for all photos; Pekin & Macfarlane 2009) taken at every sampling point

(30 pictures per transect). Pictures were analysed in a Gap Light Analyzer (GLA_v.2) with the threshold at 150.

Statistical analyses

We tested the effect of site and caterpillar feeding mode on incidence of attacks by repeated-measures ANOVA with nested design and two within-category effects. All 30 sampling points were nested in each of the four experimental sites. Percentages of attacked caterpillars were arcsine transformed. We excluded all unidentified attack attempts or lost caterpillars from the analysis. The day of experiment (from 1 to 6) was used as the first within-sampling-point effect, and feeding mode of caterpillar (semi-concealed or exposed) as the second within-sampling-point effect.

The attacks of individual predator taxa were also analysed using repeated-measures ANOVA. Repeated observations from each observation point were summed together, as the time did not show any significant impact in previous analyses. Total numbers of attacked caterpillars were logarithmically transformed (log x + 0.1). Type of predator (ant, bird, wasp, mammal, parasitoid) was used as the first effect and feeding mode of caterpillar (semi-concealed, exposed) as the second effect. Tukey post hoc tests were performed to test differences between study sites and predator taxa. Statistica 9 for Windows (Statsoft Inc., http://www.statsoft.com) was used for the analyses and graphs.

RESULTS

We exposed a total of 14 400 caterpillars, and identified 2443 attack attempts. We excluded 432 (3%) missing caterpillars from analyses, because we were not able to identify the predator. Overall percentage of attacked caterpillars was significantly lower on semi-concealed (5.44%) than on exposed (11.4%) caterpillars (Table 1, Figure 2). This was true in all types of habitat and at all times after initial exposure (Table 1). Although the number of attacks changed with time after exposure, it did not show any trends, and did not correlate with the length of experiment in any habitat (Pearson $r < 0.17$, $P > 0.05$).

Total percentage of attacked caterpillars during the whole experiment was highest (5.7%) in the lowland forest fragment in Ohu and in the montane primary forest in Kotet (4.7%), and significantly lower in the partly disturbed and primary lowland forests in Wanang (3.2%) (Figure 2, Table 2). The majority of all recorded attacks on caterpillars was by birds (6.6%) and ants (6.8%), followed by predatory wasps (1.86%), parasitoids (0.77%) and small mammals (0.77%). Individual enemies showed different numbers of attacks across sites and between semi-concealed and exposed caterpillars (Table 3).

Table 1. Effects of site (Wanang 1, Wanang 3, Oho, Kotet), feeding mode (semi-concealed or exposed), and day (from the start of experiment) on the incidences of attack on caterpillars. Repeated-measures ANOVA.

	df	F	P
Intercept	1	775	< 0.001
Site	3	13.1	< 0.001
Feeding mode	1	294	< 0.001
Feeding mode × Site	3	10.2	< 0.001
Day	5	28.3	< 0.001
Day × Site	15	7.52	< 0.001
Feeding mode × Day	5	0.84	0.519
Feeding mode × Day × Site	15	2.03	0.012

Ants, birds and wasps attacked exposed caterpillars significantly more than semi-concealed ones ($P < 0.001$ for all predator groups), while mammals ($P = 0.615$) and parasitoids ($P = 0.354$) attacked the two types of caterpillars with similar, and low, frequencies (Figure 3). For exposed caterpillars, different groups ranked by attack frequency were: birds > ants > wasps > (parasitoids = mammals) while in semi-concealed caterpillars, the incidence of attacks by (ants = birds) > (wasps = parasitoids = mammals).

Ants attacked the largest number of caterpillars in the lowland forest fragment in Ohu (11.3% = 399 ind.) and the lowest number in montane forest in Kotet (5.1% = 167 ind.). Birds were significantly more frequent predators of caterpillars in montane Kotet (12.8% = 420 ind.) than in lowland forests, where the forest fragment in Ohu (7.1% = 252 ind.) had significantly higher incidence of attacks by birds than both disturbed and primary Wanang forests (4.5% = 162 and 3.5% = 127 ind.). Parasitoids attacked significantly more caterpillars in Ohu (1.2% = 45 ind.) than anywhere else (maximum 0.7% = 27 ind. in Wanang 3, Figure 4).

In the lowlands, the canopy openness was significantly higher in disturbed forest (Wanang 1, mean ± SD = 22.5% ± 2.69%) and the primary forest fragment (Ohu, 25.3% ± 5.25%) than in the undisturbed primary forest (Wanang 3, 9.74% ± 1.49%) (ANOVA, Tukey post hoc test: $P = 0.03$). Canopy openness in the montane forest in Kotet was mid-way between that found in the disturbed and undisturbed forests (16.0% ± 2.46%).

The experiment comparing plasticine balls and plasticine caterpillars showed significant preference for caterpillars by all natural enemies (Site: $P = 0.012$, $F_3 = 21.3$; Site × Predator: $P = 0.071$, $F_{12} = 0.63$, ANOVA) as they attacked caterpillars 8.6 ± 0.5 times more than balls (0.9%) at all sites.

DISCUSSION

The results of experiments with artificial caterpillars have to be interpreted with caution. These caterpillars

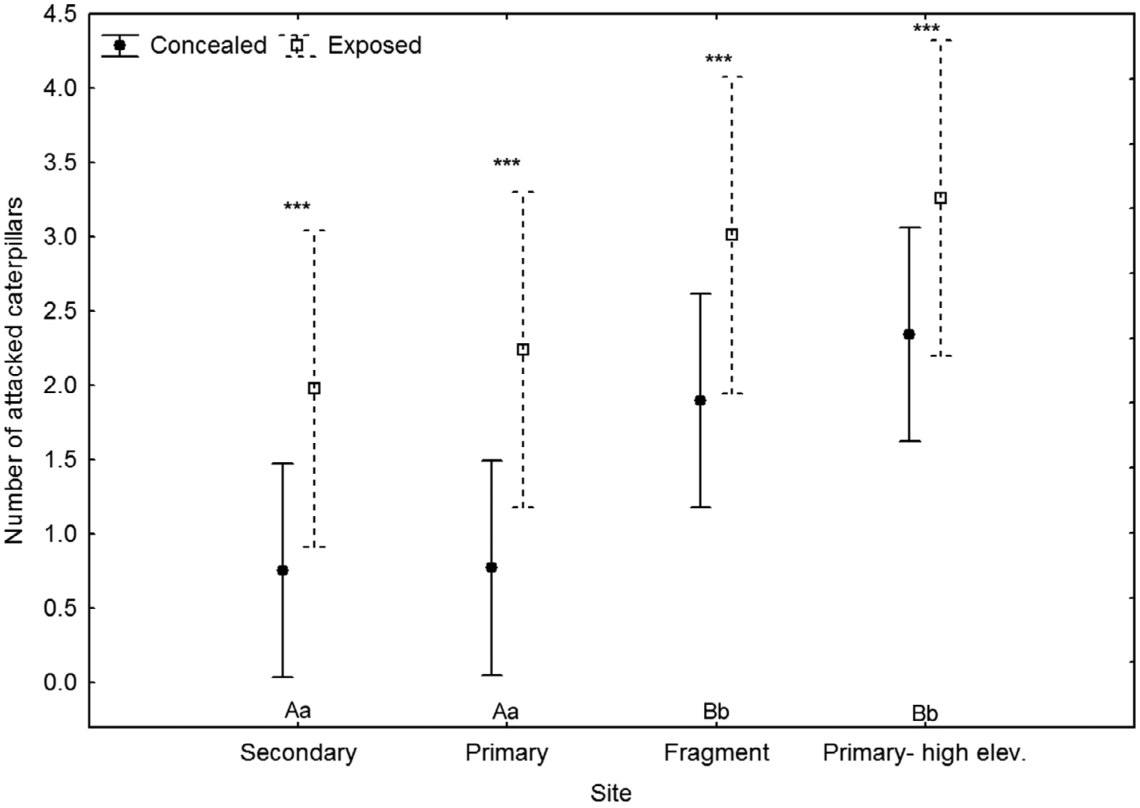


Figure 2. The number of attacks recorded after 24 h on 300 semi-concealed and 300 exposed caterpillars at different sites. Sites with significantly different rates of attack ($P < 0.05$) are denoted by different letters; capital letters = differences within semi-concealed caterpillars, lowercase letters = differences within exposed caterpillars. Differences between semi-concealed and exposed caterpillars within one site are marked with stars (*** $P < 0.001$).

provide only visual cues to their natural enemies whilst lacking chemical signals which may be important for prey recognition by some predators (Gentry & Dyer 2002, Murakami 1999, Vet & Dicke 1992, Weiss *et al.* 2004). It should be emphasized that our method samples only a tiny fraction of the parasitoid community, since many parasitoid Hymenoptera locate hosts through chemical cues (Wölfling & Rostás 2009), and numerically dominant *Tachinidae* would not leave any markings on the models as they deposit eggs onto the skin of the host insect (Stireman *et al.* 2006). The absence of motion can also eliminate attacks by some natural enemies (parasitoids: Vinson 1984; spiders: Nyffeler 1999). On the other hand, moving prey may be more vulnerable (Lima & Dill 1990). Further, the experiments measure only attack incidence whilst ignoring differential ability of prey to escape (Lima 1992) and defend itself against predators (Dyer 1997). Levels of predation by different predators exhibit significant variation (Dyer 1997, 2002; Hölldobler & Wilson 1990), and different enemy taxa also handle live insects very differently from dead or fake prey.

The incidences of attack on our exposed artificial caterpillars were similar to incidences of attack measured on genuine exposed caterpillars in exclosure experiments

Table 2. Comparison of incidence of attack at different sites. Sites: Ohu (lowland forest fragment), Wanang 3 (WA3, lowland primary forest), Wanang 1 (WA1, lowland secondary forest), Kotet (KOT, primary forest at high elevation). Tukey post hoc test results for total number of attacks, and attack by individual enemies are shown.

	Total	Ant	Bird	Parasitoid	Wasp	Mammal
OHU × WA1	0.001	< 0.001	< 0.001	< 0.001	0.999	0.066
OHU × WA3	< 0.001	< 0.001	0.041	0.001	0.999	0.961
OHU × KOT	0.701	0.002	0.718	0.002	0.999	0.456
WA1 × WA3	0.913	0.998	0.801	0.464	0.953	0.985
KOT × WA3	0.004	0.157	< 0.001	0.998	0.801	0.999
KOT × WA1	< 0.001	0.004	< 0.001	0.441	0.999	0.999

Table 3. Effects of natural enemy, site (four habitats), and feeding mode (semi-concealed or exposed) on the number of attacks on caterpillars (repeated measures ANOVA).

	df	F	P
Intercept	1	170	< 0.001
Site	3	39.6	< 0.001
Predator	4	167	< 0.001
Predator × Site	12	8.62	< 0.001
Feeding mode	1	210	< 0.001
Feeding mode × Site	3	12.1	< 0.001
Predator × Feeding mode	4	15.7	< 0.001
Predator × Feeding mode × Site	12	3.68	< 0.001

(7.5% ± 6.7%, median = 5.8%, nine studies from both tropical and temperate habitats; Remmel *et al.* 2011).
In contrast, other manipulative studies with real larvae provided higher estimates of daily attack incidence (78% in lowland forest, Brazil – Jeanne 1979, 75.5% in Costa Rica – Dyer 2002). Daily attack incidence on artificial caterpillars in a lowland seasonal forest in Barro Colorado Island in Panama was 11.1% (Richards & Coley 2007) and 42.0% (Koh & Menge 2006), 13.7% in semi-evergreen lowland dipterocarp forest in the Philippines (Posa *et al.* 2007) and 29.1% ± 23.3% d^{-1}; median = 26.6% in three studies from different tropical areas (Remmel *et al.* 2011). An extremely low predation rate of 0.03% d^{-1} was recorded on cotton fields in Uganda (Howe *et al.* 2009). It is worth noting in this context that a constant daily mortality rate of 1%, 5% and 20% would produce overall mortality of respectively 19%, 66% and 99% over 3 wk of caterpillar life span.

Overall share of attacks by arthropods (ants, wasps, parasitoids) in our study (46%) was lower than that found in some other forest studies on artificial caterpillars: 90% or greater in Koh & Menge (2006), and Loiselle & Farji-Brener (2002), but higher than 39% found in a similar study in understorey (Posa *et al.* 2007).

Our experiments using models of caterpillars do not necessarily provide an estimate of natural predation rates, but the relative number of predation incidents may be comparable among habitats (Brodie 1993). We believe that artificial caterpillar experiments serve well as a relative measure of number of attacks (Howe *et al.* 2009). Likewise, Richards & Coley (2007) found no differences between number of attacks on artificial and real undefended caterpillars.

The lower incidence of attacks on semi-concealed than exposed caterpillars by birds, ants and wasps is the strongest pattern revealed in our study, as it is consistent across all sites. At the same time the abundance of semi-concealed caterpillars in herbivore communities is high. In lowland New Guinea forest, they are more than twice as

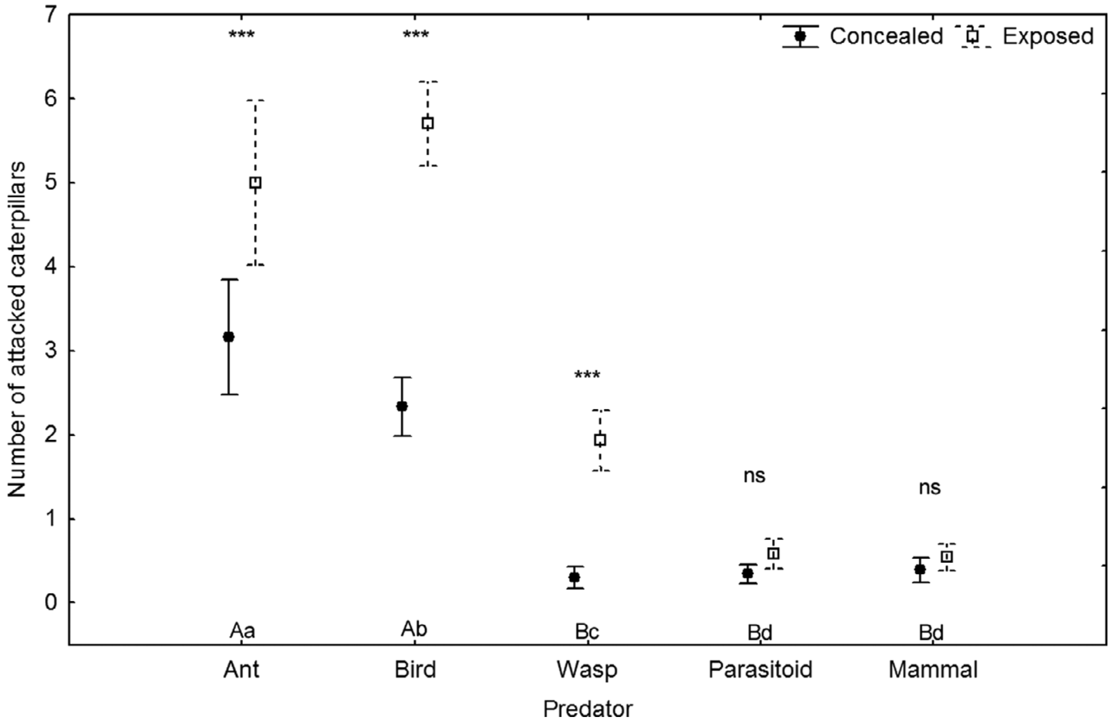


Figure 3. The number of attacks by different natural enemies recorded after 24 h on 300 on semi-concealed and 300 exposed caterpillars. Sites with significantly different incidence of attack ($P < 0.001$) are denoted by different letters; capital letters = semi-concealed caterpillars, lower-case letters = exposed caterpillars. Differences between incidence of attack of individual natural enemies on semi-concealed and exposed caterpillars are marked in stars (*** $P < 0.01$). Current effect: $F_{(4, 464)} = 31.3$, $P < 0.001$. Vertical bars denote 95% confidence intervals.

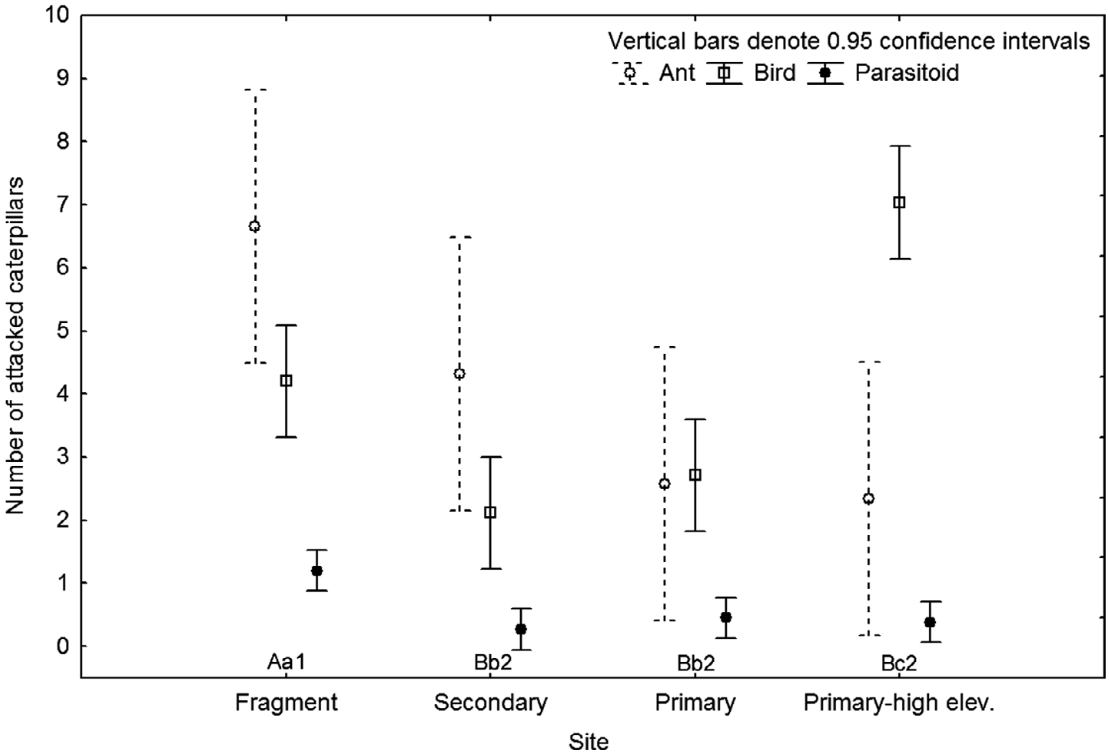


Figure 4. The number of attacks by different natural enemies recorded after 24 h on 600 caterpillars at the four experimental sites. Enemy groups with significantly different incidence of attack ($P < 0.05$) are denoted by different letters or numbers; capital letters = ants, small letters = birds, numbers = parasitoids.

abundant as exposed caterpillars (Novotny *et al.* 2012). Although there are studies showing that leaf rolls can decrease risk of predation (Atlegrim 1992, Cappuccino 1993, Loeffler 1996), their role in avoiding predation has not been quantified. Here we report that leaf refuges protect caterpillars against predation and they improve caterpillar survivorship.

The expectation was that mainly visually oriented birds prey more on exposed caterpillars, although at least some bird species specialize on leaf-rollers (Robinson & Holmes 1982). We confirmed that difference in incidence of attack between semi-concealed and exposed caterpillars was greater for birds than for other predators. This is not self-evident as equally plausibly, birds could use leaf rolls as visual cues for finding caterpillars.

The preference by ants and wasps for exposed caterpillars is in concordance with the study of Krombein (1967) of abundant social wasps (Klein *et al.* 2002) which had bigger impact on exposed than semi-concealed caterpillars, while less abundant solitary wasps fed chiefly on leaf rollers and leaf tiers in lowland tropical forest (Klein *et al.* 2002). Fowler & Macgarvin (1985) showed that free-living caterpillars were reduced in abundance more than leaf tiers on birch trees with *Formica* ants. In contrast, Ito & Higashi (1991) found similar impact of ants on both free-living and semi-concealed caterpillars.

Mammals and parasitoids did not show any significant differences in attacks on the two types of caterpillar. In terms of invertebrate biomass, caterpillars represent an important food source for rodents (Posa *et al.* 2007, Roux *et al.* 2002), however we observed very few predatory attacks by rodents on both semi-concealed and exposed caterpillars. It is well established that parasitism is much higher on concealed larvae, such as miner and gallers, than on exposed caterpillars, with semi-concealed caterpillars probably experiencing incidence of parasitism somewhere in between (Hawkins *et al.* 1997). Gentry & Dyer (2002) showed higher incidence of parasitism for semi-concealed feeders than for free-living caterpillars. Our results do not conform to this expectation, although this might be due to the low number of attacks we recorded, and hence low statistical power.

The effects of habitat alternation on predation are not well understood (Koh & Menge 2006) although there is some evidence of higher predation and parasitism in disturbed areas (Doak 2000, González-Gómez *et al.* 2006, Posa *et al.* 2007) and forest gaps (Faveri *et al.* 2008). Correspondingly, our forest fragment had incidence of attack twice those of primary and secondary forests (Wanang 1 and 3). However, our results on differences between forest types should be considered as preliminary since we did not study replicated sites for each habitat.

The lack of a difference between incidence of attack in primary and secondary forests is surprising, but could be explained by the conditions of our secondary forest at the site. We were working in a selectively logged area which also included old food gardens, and some patches of primary forest.

Externally feeding insect herbivores are exposed to intense predation pressure by ants (Hölldobler & Wilson 1990, Rodewald *et al.* 2001, Stamp & Bowers 1991), birds (Koh & Menge 2006, Posa *et al.* 2007) and wasps (Shelly 1986, Stamp & Bowers 1988) in tropical lowland rain forests. This was also true at our study sites. Predation at our sites increased with disturbance. A higher intensity of attack by ants in forest fragments could be caused by higher abundances of some invasive species or by different composition of communities (Klimes *et al.* 2011, Peters *et al.* 2009) and by higher levels of aggression of some invasive ant species (Human & Gordon 1999). Another reason could be facilitated access to forest interior in anthropogenically changed landscapes (Rodewald *et al.* 2001), greater insolation of the forest understorey causing higher activity of arthropods (Faynor *et al.* 1996, Klimes *et al.* 2011, Louda & Rodman 1996) or improved visibility facilitating caterpillar location by visually oriented enemies (Martin & Karr 1986, Valladares *et al.* 2006). Richards & Coley (2007) showed that differences in light availability could lead to dramatic changes in trophic interactions between caterpillars and their predators. Posa *et al.* (2007) found different incidence of predation in habitats with a range of canopy openness (closed-canopy forest, open-canopy forest, rural areas) and Richards & Coley (2007) found differences in predation under continuous forest canopy and in gaps. This could be a possible explanation in our case as the canopy openness was significantly higher in the forest fragment in Ohu and the secondary forest in Wanang 1 compared with the primary forest in Wanang 3, and marginally (non-significantly) higher in forest fragment than in secondary forest. Also, parasitoids attacked more caterpillars in the forest fragment than in the other habitats. This pattern mirrors other results (Valladares *et al.* 2006), and again can be explained by higher efficiency resulting from improved visibility facilitating host location, which in parasitoids seems driven also by visual clues (Salvo & Valladares 2004).

The incidence of attack at higher altitudes was higher than in lowlands, a similar result to that from temperate forests (Jeanne 1979, Mäntylä *et al.* 2008). This could also be caused by increased light availability in montane forest which facilitates predation (Martin & Karr 1986), by higher abundances of predators (Kessler *et al.* 2011), or by lower abundance of potential prey (Kessler *et al.* 2001, McCoy 1990). The highest predation caused by birds was in the montane forest, and this could be the result of a higher proportion of insectivorous birds living in the understorey of primary forest at higher elevations than in lowlands (insectivores represented 63% of all montane and 47% of all lowland species in our quantitative survey; Tvardikova unpubl. data). In contrast, Schwenk *et al.* (2010) did not find any effect of bird predation on arthropod abundance across an altitudinal gradient (290–780 m asl). The abundance of predatory wasps was also unrelated to altitude (Banko *et al.* 2002). We expected lower predation by ants in montane areas, since this group become progressively less abundant with increasing altitude and ant are already very rare at 1800 m asl (Samson *et al.* 1997). Surprisingly, predation by ants was not lower in montane forest than in some lowland forests in our study.

In conclusion, our study detected fewer attacks on semi-concealed than exposed caterpillars. We were able to identify predation attempts of birds, ants, wasps, rodents and also attacks of parasitoids on our artificial caterpillars, demonstrating the potential of this method for predation studies. The differences in relative attack pressure among the habitats from this study show that human disturbance can affect the biotic interactions between caterpillars and predators. In addition, we showed that the differences in potential predator assemblages across elevation could lead to dramatic changes in trophic interactions, with herbivores being limited by different kinds of predators in different habitats and at different elevations.

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