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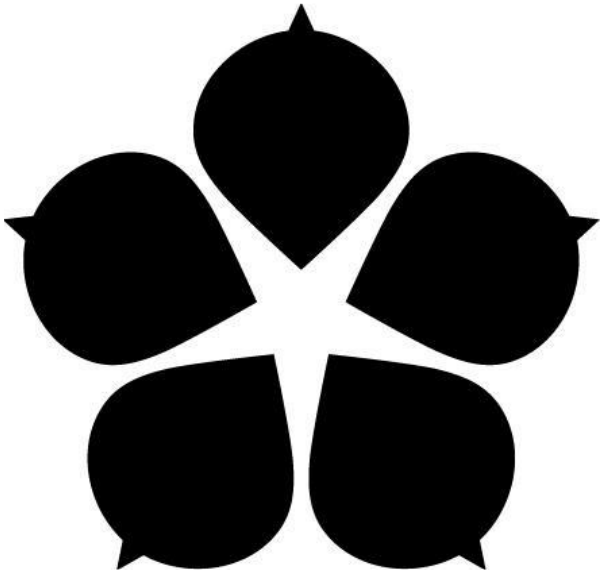

# PREDATION PRESSURE ON ARTIFICIAL CATERPILLARS INDICATES ENEMY-REDUCED TIME AND SPACE

RNDr. Thesis

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## Annotation

This thesis explores patterns of predation on artificial caterpillars in two neotropical lowland rainforest ecosystems. The specific aim was to test if enemy-reduced time and space does exist for physical undefended caterpillars. Our results indicated that larval Lepidoptera are capable to lower predation risk by nocturnal foraging and by avoiding habitats of high light irradiance. Thus, habitat-specific host plant choice by adult females and a timely scheduled foraging behaviour of the caterpillars could remarkably increase the survival rate of immature stages.

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SHORT COMMUNICATION

# Predation on artificial caterpillars is higher in countryside than near-natural forest habitat in lowland south-western Costa Rica

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**Abstract:** Predation pressure is essential in regulating population dynamics of herbivorous insects. We used artificial caterpillars (25 × 4 mm) made from brown-or green-coloured plasticine to compare predation pressure between countryside and near-natural rain-forest habitat in the Gulfo Dulce region (Costa Rica). Within each habitat, 162 caterpillars were placed randomly on different substrates along a 1200-m transect and at heights between 0.5 and 2.0 m. Artificial caterpillars were inspected at 24-h intervals for 3 consecutive days. Predation pressure was almost twice as high for countryside (mean attack frequency per capita: 1.11 ± 0.08 SE) compared with rain forest (0.66 ± 0.07 SE). In both habitats arthropods emerged as chief predator group, followed by birds. Attacks by non-volant mammals were very rare and restricted to rain-forest sites. In the countryside, bird attacks were more than four times as common as in forest, indicating a change in their relative importance across habitats.

**Key Words:** arthropod predators, artificial caterpillars, birds, Costa Rica, countryside, predation, rain forest

Throughout tropical ecosystems, herbivorous insects play an important role in their impact on plant life and nutrient cycling (Coley & Barone 1996, Massad *et al.* 2013, Metcalfe *et al.* 2014), as well as prey for their natural enemies (Ruiz-Guerra *et al.* 2012, Young *et al.* 2013). Top-down control through predation pressure (Hairston *et al.* 1960) is essential in understanding population dynamics of herbivorous insects. While a number of studies have addressed this aspect for individual habitats (Howe *et al.* 2009, Koh & Menge 2006, Richards & Coley 2007), comparisons of predation pressure between countryside and natural forest sites within the same area are rare (Posa *et al.* 2007). Large spatial distances between disparate habitat types may introduce confounding factors such as differences in climate and predator community composition. To maximize comparability, we therefore assessed predation pressure between countryside and adjacent near-natural lowland rain-forest habitat. We tested the following three hypotheses: (1) predation pressure is higher in countryside than in old-growth forest; (2) arthropods represent the main predator group in both habitat types; and (3) birds have a relatively higher impact in countryside with less canopy cover compared with forest habitats.

Our study was conducted in the Golfo Dulce region situated in the Pacific lowlands of south-western Costa Rica. Field work was carried out in proximity to the La Gamba Field Station (8°61′42″N, 83°97′12″W; 78 m asl) near Golfito in August 2014. The region is characterized by a wet season between May and November and a dry period from December to April. The average annual precipitation and temperature in this area is about 5800 mm and 28 °C, respectively (Weissenhofer & Huber 2008).

The forest site encompassed an old-growth rain forest located in the south of the Piedras Blancas National Park (140 $km^2$). This site is characterized by wet soil conditions, a clearly stratified vegetation structure, trees growing up to 30 m tall, and high canopy closure, interrupted only by occasional tree-fall gaps. Adjacent countryside habitat was characterized by a mosaic of active and fallow pastures, as well as rice fields with scattered shrubs and trees, and correspondingly low canopy cover (<20%). More comprehensive information on characteristics of the study area can be found in Weissenhofer *et al.* (2008).

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To compare predation pressure between habitat types we used artificial caterpillars. This experimental approach has become popular in recent years (Low *et al.* 2014). Artificial caterpillars (25 mm long, 4 mm in diameter) were made from oil-based non-toxic modelling clay (Koh-I-Noor Hardtmuth brand). Dark green and brown colours were used to imitate two very common colourations among undefended caterpillars (i.e. lacking urticating hairs or spines and aposematic colouration indicative of chemical defence). Within each habitat, 162 artificial caterpillars were placed on suitable structures (e.g. leaves, branches, stems) along a 1200-m transect with a minimum distance of 5 m from each other. Locations were situated 0.5–2.0 m above ground depending on accessibility, since such minor variation in height was deemed unlikely to affect predation (Koh & Menge 2006, Posa *et al.* 2007). Transects in both habitats were located at a distance of at least 50 m from the forest edge and within the same narrow altitudinal range (about 80–100 m asl). Artificial caterpillars were visited at 24-h intervals and remained in the field for 3 consecutive days. Bite marks were classified according to Low *et al.* (2014) as either arthropod, bird or small-mammal attacks.

We analysed predation pressure using Generalized Linear Models (GLMs) based on Poisson distribution and log-link function. Prior to analysis, data from locations where at least one replica was lost or showed undetermined bite marks were excluded (n = 11, 3.5%). The remaining 939 caterpillar-days comprised 151 and 162 artificial caterpillars in countryside and forest habitat, respectively. For each artificial caterpillar individual, the number of predation events across the 3 d of observation was aggregated resulting in attack scores between 0 and 3.

Neither birds nor arthropods showed a preference for one colouration over the other (Table 1). Parallel to assumptions concerning green caterpillars forwarded by Howe *et al.* (2009), this indicates that brown specimens are perceived as palatable and non-toxic by visually oriented predators in a similar manner.

During the 939 caterpillar-days of exposure, most attacks were attributed to arthropods (n = 216), followed by birds (n = 67) and small mammals (n = 3), resulting in an overall predation (mean ± SE) of 29.2% $d^{-1}$ ± 2.6% $d^{-1}$ across both habitats. Twelve artificial caterpillars were attacked by two different predator groups. Overall, our findings correspond to an intermediate predation pressure which is nearly identical to the grand mean (29.1%) across a wide range of studies reported by Remmel *et al.* (2011) for similar experiments using artificial caterpillars.

Mean number of attacks per caterpillar (± SE) accumulated over 3 d was significantly higher in countryside (1.11 ± 0.08) compared with the forest habitat (0.66 ± 0.07, Figure 1) indicating, if extrapolated to real caterpillars, that predation pressure is much higher in human-disturbed countryside than in near-natural rain forest.

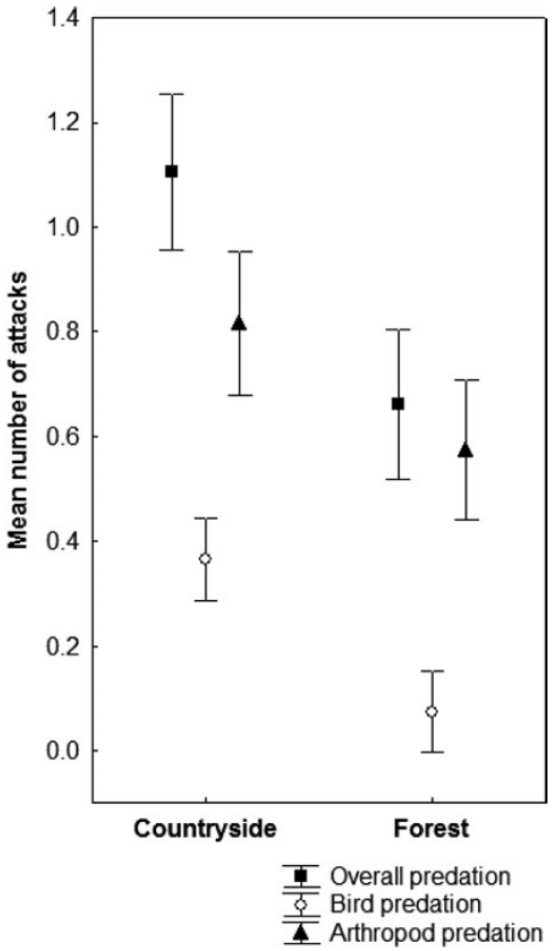


**Figure 1** Mean number of attacks (±95% CI) per caterpillar during 3 d of exposure in forest (n = 162) and countryside habitat (n = 151), Golfo Dulce region, Costa Rica. Incidences of attacks were significantly lower ($P < 0.001$) for overall predation, bird predation and arthropod predation in forest habitat (GLM, Poisson-type error structure).

Arthropods emerged as the principal predators of artificial caterpillars in both habitats (>75% of all predation events), although their mean number of attacks (± SE) accumulated over 3 d was significantly lower in the forest (0.57 ± 0.06) compared with countryside (0.81 ± 0.08, Figure 1). This is contrary to the findings of Posa *et al.* (2007) who observed higher predation by arthropods in closed-canopy forest than in rural areas in the Philippines. Ants can safely be assumed to act as chief predators of caterpillars as they are the most abundant group of predatory arthropods in the tropics (Floren *et al.* 2002, Hölldobler & Wilson 1990, Loiselle & Farji-Brener 2002, Richards & Coley 2007, Sam *et al.* 2014). Although

**Table 1.** Effects of habitat type (near-natural forest–countryside) and artificial caterpillar colour (brown–green) on mean number of attacks per caterpillar accumulated over 3 d in Golfo Dulce region, Costa Rica. Overall predation, arthropod predation and bird predation were analysed separately by GLMs with Poisson-type error structure. For all three analyses n = 313.

| | | Overall predation | | Arthropod predation | | Bird predation | |
|---|---|---|---|---|---|---|---|
| Effect | df | Wald's $Chi^2$ | P | Wald's $Chi^2$ | P | Wald's $Chi^2$ | P |
| Habitat type | 1 | 17.4 | <0.001 | 6.16 | 0.013 | 24.4 | <0.001 |
| Caterpillar colour | 1 | 0.091 | 0.763 | 0.259 | 0.611 | 0.925 | 0.336 |
| Habitat type × caterpillar colour | 1 | 2.75 | 0.097 | 2.56 | 0.110 | 1.23 | 0.267 |

species richness of ants is typically higher in mature tropical forests, ant abundance may increase with the level of disturbance, since some dominant ant species can attain very large colony sizes in open grass and shrub land (Brühl & Eltz 2010, Philpott *et al.* 2010). This may also account for the higher predation pressure in countryside observed in our present study.

Attacks by birds were significantly more common in countryside than in rain forest (mean number of attacks (± SE) accumulated over 3 d: 0.36 ± 0.05 vs. 0.07 ± 0.02; Table 1, Figure 1). The comparatively low predation by birds in near-natural forest was unexpected, since a study by Schulze & Riedl (2008) in the same research area revealed similar densities of insectivorous birds in forest habitat and neighbouring countryside. Instead of reflecting the abundance of predatory birds, our findings seem to support the suggestion by Posa *et al.* (2007) that birds may more easily locate prey in open habitat compared with closed-canopy forest. Increased predation pressure in open sites near the forest edge may consequently be due to some understorey birds foraging in adjacent habitat (Hughes *et al.* 2002). Furthermore, the relative importance of avian predators differed between habitats. Birds accounted for a third of overall predation events in countryside (32.9%), but only for 11.2% at forest sites, while arthropod attacks showed a corresponding increase from 69.1% to 86.1%. Thus, the proportional impact of birds as caterpillar predators apparently declines from countryside to forest, whereas arthropods show the opposite trend. In conclusion, our experiment revealed that caterpillars in tropical countryside habitat directly adjacent to a rain-forest reserve may experience even higher predation pressure than inside near-natural rain forest.

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# Day vs. night predation on artificial caterpillars in primary rainforest habitats – an experimental approach

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*Key words*: ants, arthropods, forest understory, gaps, nocturnal activity, predation risk, *Crematogaster*, antipredator adaptation

**Abstract**

The influence of natural enemies has led to the evolution of various predator avoidance strategies in herbivorous insects. Many caterpillars are exclusively active at night and rest during the day. It is widely assumed that nocturnal activity in caterpillars reduces their risk of falling prey to their natural enemies. To test this hypothesis, we compared predation pressure between day and night in tree-fall gaps and closed-canopy forest sites in an Amazonian primary lowland rainforest. Artificial clay caterpillars, showing camouflaged colouration (green), were exposed as potential prey to a natural predator community. Attacks were significantly more frequent during daytime and were reduced by about a quarter at night in tree-fall gaps, and by a third in closed-canopy forest sites. This supports the idea of time-dependent activity in caterpillars as an antipredatory adaptation. Further, independent of the time of day, predation pressure on caterpillars was significantly higher in tree-fall gaps compared to closed-canopy forest habitats. Nearly all predation events were caused by arthropods, whereas birds played a negligible role. Across both habitat types and time scales, ants acted as major predator group, emphasising their important role in population control of herbivorous insects in lowland rainforest ecosystems. This is the first experimental study using artificial caterpillars to examine whether time-scheduling of exposition might influence predation risk amongst undefended, solitary, free-living lepidopteran larvae.

## Introduction

Predator–prey interactions are a major driving force in the evolution of defensive traits (Reznick, 1982; Caro, 2005). Lepidopteran larvae occupy low positions in food webs. As genuine prey for a wide range of insectivores, they developed a broad range of defence mechanisms to reduce mortality risks accruing from their natural enemies. Many biochemical, physiological, morphological, and behavioural traits of caterpillars have strongly been shaped by selection through predators (Greeney et al., 2012). Behavioural adaptations of caterpillars, known as effective responses to top-down forces, include, amongst others, gregarious feeding, leaf-shelter building, or living in association with ants (Greeney et al., 2012). Caterpillars of many Lepidoptera species forage mostly during night (Heinrich, 1979) and move away from their feeding sites to hide during the day, often well camouflaged. The advantage of this behaviour is still insufficiently understood (Santana et al., 2012), as not feeding during much of available life-time is also associated with developmental costs. Nocturnal foraging could be adaptive in terms of reducing predation risk (Heinrich, 1979; Reavey, 1993). This idea is supported by the fact that times of feeding activity are more dangerous for caterpillars than times of inactivity (Bernays, 1997). Thus, predation risk may decrease by concentrating on enemy-free time to forage. Of course, an exclusively nocturnal feeding activity of caterpillars is costly due to extended developmental time and reduced growth rate (Berger & Gotthard, 2008). Thus, caterpillars of many lepidopteran species show an ontogenetic shift towards exclusive nocturnal activity with increasing body size and concomitant higher predation risk (Berger & Gotthard, 2008). Furthermore, caterpillars in later instars are more resistant to starvation (Reavey, 1993) and therefore better able to balance the cost-benefit

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ratio of extending non-feeding portions of their life time (Berger & Gotthard, 2008).

However, not only the time schedule but also the type of foraging habitat can affect the level of predation (Posa et al., 2007; Richards & Coley, 2007; Seifert et al., 2015). Accordingly, a thorough knowledge of predation pressures across spatial and temporal dimensions is necessary to understand the selective value of presumably defence-related life-history traits. It is essential to recognise the chief predator groups to evaluate the efficacy of specific antipredator adaptations.

Although some studies have documented enemy-free time and space for herbivorous insects in general (Fox & Eisenbach, 1992; Novotny et al., 1999), only few quantitative studies on focal species with unusual social life styles have investigated whether time-scheduling by caterpillars can reduce their mortality risk accruing from natural predators (Peters & Despland, 2006). Here, we compare variation in predation risk of undefended solitary lepidopteran larvae between day and night. This life style is far more typical amongst the Lepidoptera than the highly derived foraging strategies of gregarious caterpillars (Hunter, 2000). We performed our experiment in two representative tropical habitat types, tree-fall gaps and closed-canopy forest sites, of a primary lowland rainforest in French Guiana. Both habitats are characteristic for primary lowland rainforest ecosystems but very different in respect to biotic and abiotic conditions relevant to herbivorous insects. A number of plant species are adapted to gaps (Brokaw & Scheiner, 1989; Coley & Barone, 1996), in that they are tolerant to increased light intensity and temperature (Denslow et al., 1998). Because of the carbon abundance and light intensity in gaps, plant species display faster growth and leaf turnover, connected with easier sugar and lipid production through photosynthesis (Coley & Barone, 1996). Thus, gaps provide higher food availability to herbivorous insects (Richards & Windsor, 2007). Additionally, gap specialists often have poor chemical defences compared to shade-tolerant plant species, and are therefore more palatable to herbivores resulting in a much higher rate of leaf damage (Coley & Barone, 1996). However, gap and shade-tolerant specialised caterpillars are also exposed to different predator densities. Insectivorous arthropod abundance in gap and closed-canopy sites differed depending on season in tropical rainforests (Richards & Windsor, 2007). Furthermore, ants, as one of the main predator groups on herbivorous insects in tropical ecosystems (Novotny et al., 1999; Floren et al., 2002), show similar species richness and composition in both tree-fall gaps and the forest understory (Feener & Schupp, 1998), whereas their densities can vary between these habitats (Richards & Coley, 2007).

Based on the theoretical conjecture of lower night-time predation (Heinrich, 1979) as well as on former studies by Richards & Coley (2007) and Loiselle & Farji-Brener (2002), we tested the following three hypotheses: (1) predation is lower during night time, (2) predation pressure is higher in tree-fall gaps compared to closed-canopy forest habitats, and (3) arthropods, especially ants, act as major predator group in tropical lowland habitats.

To avoid confounding traits of arbitrarily selected focal test prey species, we instead used artificial caterpillars. This is a suitable method to compare relative predation pressure along ecological contrasts including a wide range of predatory guilds (Loiselle & Farji-Brener, 2002; Low et al., 2014; Howe et al., 2015).

## Materials and methods

### Study site

We conducted our study during the dry season at the Nouragues Nature Reserve (French Guiana) in northern Amazonia between 25 October and 16 November 2014. The reserve comprises around 1 000 km² of hilly primary lowland rainforest (terra firme), showing a mosaic of ridges, creeks, and a complex drainage system. Our study sites were situated in close proximity to the camp 'Saut Pararé' (4°02′N, 52°41′W, 78 m a.s.l.; Nouragues Ecological Research Station), located some 100 km inland next to the Arataye River. The climate is tropical humid with a wet season from December to June and a dry season from July to November. Average annual temperature and precipitation in this area are about 26.3 °C and 2 990 mm (Grimaldi & Riéra, 2001). More information about the study area can be found in Bongers et al. (2001a).

We chose two common habitat types of natural rainforests, tree-fall gaps and closed-canopy forest sites. Each site of both habitats occupied an area of around 100–150 m². The forest at the later old study sites was well stratified, showing an average tree height of around 40 m (Dubois-Fernandez et al., 2012), resulting in nearly closed canopy and very low levels of solar irradiance reaching the forest floor. We selected tree-fall gaps with regrowth not more than 2 m high. Canopy openness of gaps on this successional level is more than 4× higher than in mature forest sites (Bongers et al., 2001b). Thus, both habitat types differ strongly in vegetation structure, irradiance, and microclimate. These parameters have been shown to affect species composition of plant and animal communities.

### Experimental design

Artificial caterpillars made of dark green oil-based non-toxic modelling clay – Koh-I-Noor Hardtmuth;

following Tvardikova & Novotny (2012) and Seifert et al. (2015) – were used to simulate undefended, cryptic, and solitary-living lepidopteran larvae in order to compare predation pressure by natural enemies during the day vs. the night, and between forest and gap sites. Tvardikova & Novotny (2012) showed that the plasticine material itself does not attract ants. Therefore, this simple experimental design is suited to reflect relative predation pressure for spatial and temporal comparisons (Loiselle & Farji-Brener, 2002; Richards & Coley, 2007; Howe et al., 2009).

We employed cryptically coloured dummies because this signals palatability and absence of specific defence mechanisms to potential predators (Howe et al., 2009). All artificial caterpillars were 30 mm long and 4 mm in diameter. We used this rather small size because many free-living, undefended macrolepidopteran caterpillars switch to exclusively nocturnal activity for foraging in later instars (Reavey, 1993; Berger & Gotthard, 2008). Accordingly, our caterpillars, for example, mimic later stages of midsize free-living noctuid, notodontid, or geometrid moth species, which are known to collectively constitute a very substantial fraction of Neotropical rainforest moth assemblages. Artificial caterpillars were placed at least 1.5 m apart on various woody plants between 0.5 and 1.5 m above ground, fixed to the midrib of leaves with insect pins.

Eight tree-fall gaps were chosen with a minimum distance of 50 m to the nearest neighbour. Every gap site was associated with one closed-canopy forest site in the immediate vicinity but at a distance of at least 15 m. At each of the 16 sites, 40 artificial caterpillars were exposed for 48 h, consisting of two consecutive day and night periods. Half of the caterpillars per site were exposed in the evening (around 18:15 hours), the other half the following morning (around 06:15 hours). Because weather could affect intensity of predation, we always exposed caterpillars simultaneously in a closed-canopy forest and its associated tree-fall gap site. Because of nearly identical lengths of day and night time, artificial caterpillars were surveyed at 12-h intervals during sunrise and sunset (around 06:15 and 18:15 hours, respectively). Thus, each caterpillar was exposed for roughly 24 day-time and 24 night-time hours. During each observation, artificial caterpillars were examined for characteristic predator bite marks. Artificial caterpillars which showed signs of predation were replaced by a new one on exactly the same position. Following Low et al. (2014), incidences of predation were classified as bird or arthropod attacks. Furthermore, predation by ants, either detected via direct observation or by characteristic bite marks, was recorded as a distinct event type.

### Statistical analysis

We compared day and night predation in old-growth forest and gap sites using generalised linear mixed models (GLMMs) based on a binomial distribution with logit link function and adaptive Gauss-Hermite quadrature (nAGQ = 20) for parameter estimation. For each artificial caterpillar, incidence of predation as the dependent variable was coded as presence/absence after two observation units for day and night. Habitat type, time period, and their interaction were modelled as fixed categorical predictor variables and the eight site pairs were included as random factor. Prior to analyses, we checked that predation data were not affected by overdispersion. One artificial caterpillar was missing during one night period and thus excluded from the GLMM analysis. For all analyses, R v. 3.2.0 (R Core Development Team, 2015) and the lme4 package (Bates et al., 2014) were used. Significance of results was assessed based on Wald's Z statistic.

## Results

In our experiment, 334 out of 640 artificial caterpillars (52.2%) were attacked at least once by arthropods or birds within 48 h of exposure. We observed a mean (± SE) daily total predation rate across both habitat types of 34.5 ± 0.02%. Significantly fewer attacks occurred during the night period in both gap and closed-canopy forest habitat ($Z = -4.53$, $P<0.001$). The proportion of predated artificial caterpillars was 25.6 and 35.4% lower during the night for gap and forest habitat, respectively (Table 1). In comparison to closed-canopy forest, tree-fall gaps showed a significantly higher predation pressure on artificial caterpillars for day and night period, respectively ($Z = 3.83$, $P<0.001$). There was no significant interaction between time period and habitat type ($Z = 0.45$, $P = 0.65$).

**Table 1** Mean (± SE) overall and ant predation on artificial caterpillars during day and night periods, in eight closed-canopy forest and tree-fall gap sites (Nouragues Nature Reserve, French Guiana). Each artificial caterpillar was exposed for 24 day and night hours (n = 640)

| Habitat type | Time period | Overall predation (%) | Ant predation (%) |
|---|---|---|---|
| Tree-fall gap | Day | 45.0 ± 2.8 | 23.1 ± 2.4 |
| | Night | 33.5 ± 2.6 | 20.4 ± 2.3 |
| Closed-canopy forest | Day | 35.3 ± 2.7 | 12.2 ± 1.8 |
| | Night | 22.8 ± 2.3 | 11.3 ± 1.8 |

Neither for overall predation nor for ant predation, there was an interaction between habitat type and time period (GLMM, binomial distribution: overall predation: $Z = 0.45$, $P = 0.65$; ant predation: $Z = -0.23$, $P = 0.82$).

Altogether we observed 533 individual attack events. On eight occasions, artificial caterpillars displayed characteristic bite marks of birds (1.5%) whereas all other attacks were attributed to arthropods (98.5%). Ants were responsible for more than 50% of all predation events by arthropods. All ants directly observed attacking artificial caterpillars belonged to the genus *Crematogaster*. Additionally, we observed differences in predator guild composition between time periods and habitat types. Attacks by birds occurred only during daytime at an equally low number of four predation events in either habitat. Thus, incidences of night-time predation were exclusively due to arthropods. In tree-fall gaps as well as closed-canopy forest habitats, the number of observed attack marks due to ants were slightly higher during daytime, but this difference was not significant ($Z = -0.90$, $P = 0.37$; Table 1). By contrast, the impact of ants as predators on artificial caterpillars differed significantly and was stronger in tree-fall gaps than in closed-canopy forest sites ($Z = 4.87$, $P<0.001$; Table 1).

## Discussion

This study demonstrates that predation pressure on artificial caterpillars during the dry season in a primary lowland rainforest ecosystem depends on habitat type and exposure time. The composition of predator groups also differed between habitats and time periods.

Considering other studies performed with artificial caterpillars in the understory of Amazonian lowland forests, there is pronounced variation in attack rates. Whereas Loiselle & Farji-Brener (2002) reported even higher proportions of daily attacks (51.3%) from the Peruvian lowlands, Fáveri et al. (2008) observed percentages ranging only from 4.2 to 10.6% in Brazil. Thus, our findings appear to indicate an intermediate predation pressure.

In our study, arthropods accounted for 98.5% of predation events. Especially ants acted as major enemies, as commonly found in tropical rainforests (Novotny et al., 1999; Floren et al., 2002; Loiselle & Farji-Brener, 2002; Sam et al., 2015a). Most ant attacks were due to species of the genus *Crematogaster*, which is highly prevalent in tropical forests (Longino, 2003). In accordance with other studies conducted in Neotropical lowland forests (Richards & Coley, 2007; Fáveri et al., 2008; Seifert et al., 2015), our findings indicate that birds play a lesser role as predators of caterpillars in understory of closed-canopy sites and small tree-fall gaps, whereas their importance can increase in more open habitats. In contrast to other Neotropical studies reporting at least occasional incidences, we did not observe predation by small mammals (Loiselle & Farji-Brener, 2002; Posa et al., 2007; Seifert et al., 2015). This is particularly surprising, as especially gleaning bats are an important predator group for herbivorous insects in the Neotropics (Kalka & Kalko, 2006). Possibly, dummy caterpillars are inappropriate to capture predation pressure on caterpillars by gleaning bats.

As nearly all attacks were due to arthropods, the observed differences of predation pressure between day and night-time period and habitat types must be interpreted with regard to this group. In this context, it is important to note that the use of artificial clay caterpillars underestimates the real predation risk of caterpillars, because specialist arthropod enemies using chemical signals in prey location (such as most parasitoids) are excluded (Sam et al., 2015a,b). This underestimation, however, is partially offset by the concomitant lack of evasive strategies adopted by living caterpillars (e.g., dropping off the host plant, head-flicking, regurgitation of foregut content, or repelling; Greeney et al., 2012).

In our experiment, predation risk was reduced by about a quarter during night-time within tree-fall gaps and by about one-third in the forest understory sites. This is in accordance with a study by Novotny et al. (1999), who observed a 3× higher predation risk during day by using termites as live baits in a lowland rainforest of Papua New Guinea. The lower predation pressure during night-time within tree-fall gap and closed-canopy forest habitats leads us to suggest that exclusively nocturnal foraging in caterpillars can strongly reduce their rate of mortality inflicted by arthropod enemies.

If only confirmed ant attacks are taken into account, there was no difference between day and night in either habitat. This is not surprising as a study by Kaspari & Weiser (2000) revealed that ant activity in tropical rainforests is not overall influenced by time of day but instead tends to vary across seasons and species. Thus, the observed higher level of day-time predation was likely caused by arthropods other than ants. In similar tropical studies involving dummy caterpillars, predatory wasps comprised the second most important group of predators besides ants (Fáveri et al., 2008; Tvardikova & Novotny, 2012; Sam et al., 2015b). Furthermore, wasps predating caterpillars are primarily diurnal (Warrant, 2008). Therefore, we assume that predatory wasps were the predominant predator group responsible for the distinctly higher predation pressure during daytime in our study.

The observed higher predation pressure on artificial caterpillars in tree-fall gaps compared to closed-canopy forest corresponds to an earlier study by Richards & Coley (2007), and is supported by increased activity of predaceous arthropods in gaps (Richards & Windsor, 2007). However, our study is the first to show that this is true for both day and night-time. One reason for the lower

predation rate within closed-canopy forest understory may be a lower abundance of ants. This is in line with the observed increase of ant attacks in tree-fall gaps and corresponds to findings by Richards & Coley (2007). A second explanation, especially valid for daytime predation, would be that predators which employ visual cues when hunting (e.g., wasps, stinkbugs, beetles, etc.) may detect their prey more easily in gaps because of higher light intensity. Most likely, differences in predation pressure between habitats are caused through a combination of both aspects.

Gaps represent small habitat islands within the rainforest with specific resources. A range of specialised shade-intolerant plant species occur only in these habitats (Brokaw & Scheiner, 1989). Consequently, undefended solitary caterpillars which rely on such plants as their specific hosts are expected to experience an intrinsically higher predation pressure compared to caterpillars exploiting more shade-tolerant plant species, independent from the exact timing of their feeding activity.

Overall, we could confirm our assumption that predation on artificial caterpillars during daytime is significantly higher than during night, in tree-fall gaps as well as in closed-canopy forest sites. Although several similar studies have thus far dealt with comparisons between habitats, this was the first experimental approach using artificial caterpillars to specifically compare levels of predation between day and night, thus addressing the search for enemy-free time. Our results support the idea that exclusively nocturnal feeding activity, which is often observed in undefended solitary caterpillars, evolved primarily as a strategy to reduce predation risk.

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