

Rapid Assessment of Lepidoptera Predation Rates in Neotropical Forest Fragments¹

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ABSTRACT

The mechanisms underlying responses of invertebrates to forest edges remain poorly understood. Here, we use an experimental approach to investigate the predation rates on butterflies in two neotropical forest fragments. Neither distance from forest edge nor degree of forest openness affected predation rates on artificial caterpillars. The mean predation rate of artificial caterpillars on Barro Colorado Island (1500 ha) was significantly higher than that on Peninsula Gigante (2600 ha) likely due to density-dependent effects. Our study demonstrates the utility of artificial predation experiments for rapid assessment of relative lepidoptera predation rates in tropical forests.

RESUMEN

Los mecanismos subyacentes de como los invertebrados responden a los bordes del bosque permanecen poco entendidos. En este estudio usamos un enfoque experimental para investigar las tasas de depredación en mariposas en dos fragmentos de bosque neotropical. Las tasas de depredación de orugas artificiales no fue afectado por la distancia al borde del bosque ni por la densidad del bosque. El promedio de depredación en orugas artificiales que encontramos en la Isla de Barro Colorado (1500 ha) fue apreciablemente más alto que en Península Gigante (2600 ha), probablemente debido a efectos dependientes de la densidad. Nuestro estudio demuestra la utilidad de experimentos artificiales de depredación para la evaluación rápida de tasas relativas de depredación en lepidópteros en bosques tropicales.

Key words: butterfly; conservation; deforestation; extinction; fragmentation; habitat loss; relaxation; tropics.

ECOLOGICAL CONSEQUENCES OF FOREST FRAGMENTATION (*i.e.*, the breaking up of a continuous forest into isolated patches) have been well studied over the past two decades (Wilcove *et al.* 1986, Laurance 1991, Saunders *et al.* 1991, Fahrig 2003). Forest fragmentation could negatively impact biodiversity through the creation of forest edges, where unfavorable microclimatic conditions (*e.g.*, elevated wind speed) and changes in biotic interactions (*e.g.*, enhanced predation pressure) could drive the decline and local extinction of forest species (Wilcove *et al.* 1986, Laurance 1991, Fahrig 2003). Previous studies of forest edge effects have focused mainly on vertebrates, especially birds (*e.g.*, Martin and Joron 2003). For example, artificial nest predation experiments have been widely used to investigate the reproductive success of birds in forest edges (*e.g.*, Wilcove *et al.* 1986, Piper & Catterall 2004). In comparison, the responses of invertebrates to forest edges, as well as the ecological mechanisms underlying those responses (*e.g.*, predation), remain poorly understood. Recently, artificial predation experiments have been used to measure predation on insect herbivores (Brodie & Moore 1995, Loiselle & Farji-Brener 2002, P. D. Coley, pers. comm.) as well as snakes (Brodie 1993, Brodie & Janzen 1995, Hinman *et al.* 1997, Pfennig *et al.* 2001) in tropical forests. Here, we use a similar experimental approach to test three hypotheses regarding the responses of tropical butterflies to forest fragmentation: (1) that caterpillar predation rate decreases from forest edge to interior; (2) that caterpillar predation rate is higher in forest gaps than under forest canopy; and (3) that caterpillar predation rate is higher on a true island than in a forest fragment.

We conducted our study in January 2005 in two tropical forest fragments in the Barro Colorado Nature Monument (BCNM), Panama (9°9'N, 79°51'W): Barro Colorado Island (BCI) and Peninsula Gigante (PG), which are administered by the Smithsonian Tropical Research Institute (Leigh 1999). BCNM has a mean annual rainfall of *ca* 2600 mm and mean annual temperature of 27°C (Leigh 1999). The vegetation in the study sites is primarily tropical moist forest (Holdridge 1947). BCI (1500 ha) was isolated from the mainland between 1910 and 1914 by the construction of the Panama Canal, whereas PG (2600 ha) was fragmented around 1990 by forest clearing (Leigh 1999). More detailed site descriptions can be found in Croat (1978) and Leigh (1999).

To capture the bite marks of potential predators, we constructed artificial caterpillars using modeling clay (Van Aken brand), which is an oil-based, nontoxic, and nonhardening modeling compound. Since the model is malleable, disturbance types can be identified from impressions upon model retrieval (Brodie 1993). Artificial caterpillars were loosely modeled after a native butterfly species, *Anartia fatima*, which is a common species at both BCI and PG (pers. obs.). Although artificial caterpillars are of an approximate match to real *A. fatima* caterpillars in terms of body size (30 mm × 8 mm), shape (cylindrical), and color (dark brown), artificial caterpillars do not possess body spines, which are present on real caterpillars, and do not give the same chemical cues as *A. fatima*. Therefore, our data may more accurately represent relative predation rates on prey of similar size, shape, and color of *A. fatima* than on *A. fatima* itself. Hereafter we refer to models as caterpillars for simplicity.

The Thomas Barbour trail on BCI was well suited to assess the effects of forest edges on caterpillar predation rates because

¹ Received 28 February 2005; revision accepted 14 April 2005.

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the trail runs relatively straight from forest edge to interior in an east to west direction. Along the Thomas Barbour trail, sampling stations were located at 0, 100, 200, 300, and 400 m inland from the forest edge. Each sampling station consisted of three sampling points, one located on the trail and one each at 50 m north and south of the trail. Within a 5 m radius of each sampling point, five artificial caterpillars were randomly attached to unobstructed parts of the vegetation (*e.g.*, upper surface of leaves or stems) at 1–2 m above ground using super glue. Each artificial caterpillar was placed on a different plant located at least 1 m apart. We recorded the type (*e.g.*, stem or leaf) and height of the substrate on which each caterpillar was attached. Each sampling point was inspected after 48 h. Each caterpillar was carefully examined for characteristic bite marks. Digital photographs of caterpillars were taken to identify the cause of bite marks with the help of Professor P. D. Coley at the University of Utah. An artificial caterpillar was recorded as depredated if it showed bite marks of potential predators (*e.g.*, ants and birds; Fig. 1a). Caterpillars that were missing were excluded from the analyses as their status could not be ascertained (<3% of total sample). Caterpillars that had bite marks of unknown causes (<5% of total sample) were assumed to be attacked by potential predators and were included in our analyses as such.

To compare caterpillar predation rates between forest gap and under forest canopy, two natural forest gap sites and two under forest canopy sites were randomly selected along the Robert K. Enders trail on PG. Additionally, the clearing of the Smithsonian Tropical Research Institute field station on PG was included as an artificial forest gap for comparison with the other sites. All sites were located at least 200 m apart to ensure independence of samples. Within each site, three sampling points (50 m apart) were located. Five artificial caterpillars were placed in each sampling point and inspected after 48 h as described above. A randomly selected sampling point within each site was sampled for butterflies, birds, and vegetation as described above. To compare caterpillar predation rates between BCI and PG, we tested for significant difference between the mean predation rate of all 15 samples on BCI and that of 12 samples (excluding three artificial forest gap samples) on PG.

Each sampling point located on both BCI and PG was also surveyed for real adult butterflies and birds. A single observer recorded all butterflies seen within a 5 m radius plot at each sampling point. Similarly, a single observer recorded all birds seen or heard within a 25 m radius plot at each sampling point. Additionally, the following vegetation characteristics were recorded within a 5 m radius plot at each sampling point: estimated percentage canopy cover; estimated maximum canopy height; number of stems above 10 cm diameter at breast height; estimated percentage cover of shrub vegetation up to 2 m above ground (estimated); and number of flowering shrubs.

A total of 68 out of 150 artificial caterpillars (45%) were attacked within 48 h (Fig. 1a). To determine whether the probability of predation was significantly influenced by the type of substrate on which the caterpillars were attached or the height at their point of attachment, we fitted binary logistic regression (logit) models on the predictor variables of substrate type (*i.e.*, leaf or stem) or height at point of attachment, and the response variable of caterpillar predation. Our results showed that caterpillars attached on stems were

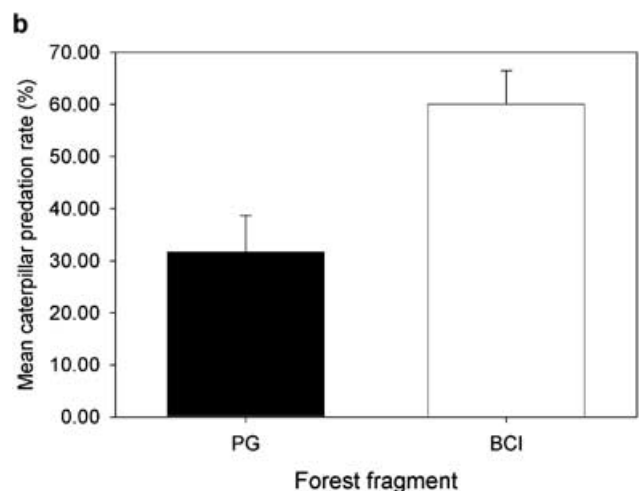


FIGURE 1. (a) Examples of different bite marks found on artificial caterpillars. (b) Comparing mean caterpillar predation rates between PG and BCI. Error bars represent standard errors.

1.9 times more likely to be depredated than those attached on leaves ($N = 145$; log-likelihood = -97.63 ; $P = 0.05$). The height at the point of attachment did not affect the probability of predation ($N = 145$; log-likelihood = -98.39 ; $P = 0.14$).

By fitting a simple linear regression model on the predictor variable of distance from forest edge and the predictor variable of caterpillar predation rate, we determined that predation rates on artificial caterpillars on BCI did not vary significantly as a function of distance from forest edge ($N = 15$; $R^2 = 0.028$; $P = 0.26$), although our results indicated a slight positive trend from forest edge to interior. Mean predation rates of artificial caterpillars at the different distances from forest edge were not significantly correlated with either species richness or abundance of butterflies or birds ($N = 5$; Spearman correlation $P > 0.05$). Mean caterpillar predation rates were also not significantly correlated with any of the vegetation characteristics measured ($N = 5$; Spearman correlation $P > 0.05$).

We performed an Analysis of Variance (ANOVA) to test for the effect of canopy openness on caterpillar predation rates. Our results showed that predation rates on artificial caterpillars were not significantly different between natural forest gap and under forest canopy (ANOVA $F_{1,10} = 0.81$; $P = 0.39$). None of the caterpillars in the artificial gap suffered any depredation. Additionally, we performed an ANOVA and determined that the mean predation rate of artificial caterpillars on BCI (60.0%) was significantly higher than that on PG (31.7%) (ANOVA $F_{1,25} = 8.60$; $P = 0.01$; Fig. 1b).

A major limitation of artificial predation experiments is that they might not reflect natural predation rates (Brodie 1993, Berry & Lill 2003), due in part to differences in sensory cues given by artificial and actual prey (Brodie 1993). Visual cues (color and ring pattern) have been shown to affect predation on artificial millipedes (Brodie & Moore 1995) and snakes (Brodie 1993, Brodie & Janzen 1995, Hinman *et al.* 1997) by avian predators, and it is likely that chemical cues would affect predation on artificial caterpillars by arthropods. Nevertheless, such predation experiments allow for a standardized, rapid assessment of relative predation rates (Brodie 1993), which is especially critical for conservation in the tropics where forests are being destroyed at unprecedented rates and where long-term studies are often limited by scarce resources (Laurance 1999). Although the probability of predation was significantly affected by the substrate on which the caterpillars were attached, our results and conclusions are not likely to be affected because the caterpillars were randomly attached to substrates at each of the sampling points, resulting in approximately equal numbers of caterpillars on both substrates. Nevertheless, to minimize this potential bias, we recommend that substrate type be standardized in future experiments. Despite the small sample size in our study, the overall caterpillar predation rate in this study (42%) was similar to that of a lowland forest understory in the Peruvian Amazon (51% predation within 24 h) that used the same techniques (Loiselle & Farji-Brener 2002). Additionally, both studies recorded high proportions of predation by arthropods (94% in this study; 90% in Loiselle & Farji-Brener [2002]).

Our results do not support either of our first two hypotheses: neither the distance from forest edge nor the degree of forest openness affected predation rates on artificial caterpillars. The difference in caterpillar predation rates between BCI and PG could be due to density dependent effects. Because BCI had a lower mean butterfly density (*i.e.*, number of individuals per plot) (1.40 ± 0.68 ; mean \pm S.E.) than PG (6.20 ± 1.20), the predation pressure on individual butterflies was likely higher on BCI than PG. This difference in butterfly density between BCI and PG could reflect the different extent of butterfly fauna relaxation since their isolation. Our study demonstrates the utility of artificial predation experiments for rapid assessment of relative lepidoptera predation rates in tropical forests.

ACKNOWLEDGMENTS

We are grateful to N.C. Gregory, R. Chaplin, J. Adelman, A. de Froment, M.M. Ramos, J.S.G. Choo, P.D. Coley, D.S. Wilcove, T.M. Lee, and N.S. Sodhi for their assistance and discussion. We thank the staff at the Smithsonian Tropical Research Institute for their support. We also thank P. DeVries and two anonymous reviewers for their comments. This research was conducted as part of a tropical ecology field course supported by the Department of Ecology and Evolutionary Biology, Princeton University.

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