Predation on artificial nests and caterpillar models across a disturbance gradient in Subic Bay, Philippines

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Abstract: One possible mechanism underlying species losses in the tropics is an increase in predation due to habitat degradation. Relative levels of predation at three heights (ground, 1–1.5 m, > 5 m for nests and > 3 m for caterpillars) were compared across a gradient of disturbance in the Subic Bay Watershed Forest Reserve, Philippines over a 2-mo period. Four 750-m transects were established in each habitat type (closed-canopy forest, open-canopy forest, rural areas) where artificial nests and caterpillar models were placed within 10-m-radius plots and checked after a 5-d exposure period. Nests in open-canopy forest were least predated (16.7%), with predation in rural areas (58.3%) being higher than in closed-canopy forest (32.8%). Predation on nests at 1–1.5 m was significantly lower than ground nests. General linear mixed model analysis suggested that effects of habitat type on nest predation differed among heights. Attacks on caterpillars increased with disturbance (46.1–59.4%), but height was not found to have a significant effect on predation. Markings on plasticine models, camera traps and live traps were used to establish possible predators. Shifts in predator dominance among the habitats were observed. Vegetation cover, tree density and small mammal abundance were not correlated with mean predation in the transects.

Key Words: deforestation, habitat disturbance, predation, reproductive success, South-East Asia, tropics

INTRODUCTION

The loss and degradation of natural habitats are driving the declines and extinctions of many tropical forest species (Brook *et al.* 2003). Habitat disturbance may impact species by causing direct mortality, reducing survivorship or decreasing reproductive success (Schlaepfer *et al.* 2002, Sih *et al.* 2000, Sodhi *et al.* 2004). All three ecological processes are potentially affected by predation. Predation is the main mechanism underlying nest mortality in birds (Ricklefs 1969) and larval mortality in butterflies (Feeney *et al.* 1985), and thereby has a strong influence on habitat selection, community structure and the distribution of species across different habitats (Martin 1988, Morris 2003, Shiojiri & Takabayashi 2003, Sieving & Willson 1998). Patterns of predation can be affected by anthropogenic changes in the landscape (e.g. fragmentation), which often increase predator abundance and facilitate their access to the forest interior (Rodewald & Yahner 2001). Information on how disturbance affects such ecological processes is largely lacking in South-East Asia (Sodhi & Brook 2006), where deforestation continues at elevated rates (Achard *et al.* 2002). Few studies on the effects of habitat disturbance on predation have been conducted in the region (for exceptions see Cooper & Francis 1998, Sodhi *et al.* 2003, Wong *et al.* 1998). For the Philippines, identified as a biodiversity hotspot due to its high levels of endemism coupled with extensive deforestation (Myers *et al.* 2000), altered predation patterns resulting from disturbance could negatively impact native fauna.

Because actual predation events are rarely observed, previous studies have used artificial models to evaluate predation pressure (e.g. for nests, Wilcove 1985; for caterpillars, Koh & Menge 2006). The use of artificial models permits the testing of specific hypotheses (e.g. effects of habitat type) by experimentally controlling for the effects of other factors, such as prey density. However, this method is subject to many inherent biases (Major & Kendall 1996), chief of which is that rates of attack on artificial models may not accurately reflect actual rates of predation (Berry & Lill 2003, Zanette 2002). Despite

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the potential limitations, the use of artificial models is a valuable tool for the rapid assessment of relative predation pressure across sites of interest, especially in regions where long-term studies are logistically or economically prohibitive (Koh & Menge 2006, Loiselle & Hoppes 1983).

Predation pressure may vary both between and within habitats (i.e. between microhabitats) due to differences in predator assemblages and density, vegetation structure and complexity, and intensity of human activities (Loiselle & Farji-Brener 2002, Martin 1993a). We used artificial models to examine the relative levels of predation on bird nests and lepidopteran larvae across three habitats that varied in levels of human disturbance in the Philippines. We also compared predation across three microhabitats of different heights (ground, 1–1.5 m and > 3 m). Based on previous studies, we expected predation pressure to (1) increase with increasing disturbance for both nests and caterpillars; and (2) be highest at ground level for nests and at the heights > 3 m for caterpillars. Our study provides empirical information on the ecological processes underlying species declines and extinctions in habitats undergoing disturbance.

METHODS

Study site

We conducted the study at the Subic Bay Watershed Forest Reserve in west central Luzon, Philippines. The 9856-ha reserve ($14°45.0'$–$14°51.0'$N, $120°15.5'$–$120°15.0'$E) was part of the former US Naval Reservation until 1992. Climate is characterized by the Type I Coronas classification (Coronas 1920), with a distinct dry season from November to April and majority of rainfall occurring during the wet months of June to September. The vegetation in the reserve is semi-evergreen lowland dipterocarp forest (Mallari *et al.* 2001), which has been subjected to various degrees of disturbance from past military activities, as well as to pressures from current developments (see Posa & Sodhi 2006 for more details). Three habitat types were distinguished based on land-use categories: (1) closed-canopy forest consisting of mature trees with canopy cover of 40% or more (4342 ha); (2) open-canopy forest that has a discontinuous tree layer and canopy cover of 10–40% (3363 ha); and (3) rural areas consisting of previously forested land now vegetated with regenerating scrub, grasslands, agricultural crops and reforestation plots (621 ha).

Predation set-ups

Predation experiments were conducted from late April to early June 2005, a period approximating the breeding season of majority of the birds in the reserve (Dickinson *et al.* 1991). Artificial nests (10 cm diameter, 6 cm depth) woven from stems of climbing ferns, *Lygodium* sp., were immersed in boiling water and dried outdoors to reduce odours prior to use. One quail (*Coturnix coturnix* Linnaeus) egg and one plasticine egg, painted to resemble a real egg, were placed in each nest. Quail eggs were obtained at a local market so that none was more than 1 wk old. Artificial caterpillars (35 mm length, 5 mm width) were made from green plasticine and painted to resemble the fifth instar larva of *Papilio alphenor* Eschscholtz, before being glued to a bamboo skewer for ease of attachment in the field.

In each habitat, four 750-m transects were randomly established, each with fifteen 10-m radius plots separated by 50-m intervals. Transects were located at least 150 m away from the forest edge. Within each plot, nests and caterpillars were randomly placed at three heights: ground, 1–1.5 m and > 5 m for nests and > 3 m for caterpillars, with one nest and caterpillar placed at each height category. Nests and skewers were secured to stems and branches using thin-gauge wire. A small piece of flagging tape was used to mark the centre of the plot. No attempt was made to conceal the set-ups to avoid any biases related to differences in concealment effort. The set-ups were checked after a 5-d exposure period. Nests were considered depredated if one or both eggs were missing, if the real egg was broken or cracked, or if there were any bite or bill marks on the artificial egg (Söderström *et al.* 1998). Caterpillars were considered predated if they were missing or had distinct beak or bite marks. All predated plasticine models were collected to identify predators from the marks made. The percentage of vegetation cover at three vertical strata (0–1 m and 1–2 m cover estimated visually; canopy cover measured with a spherical densiometer) and the number of trees with dbh > 4 cm were recorded within each plot.

Predator identification

A variety of techniques were used to identify potential predators. When checking set-ups, effort was expended to retrieve any eggshell or model remains, and to record any animal traces. Markings on the plasticine models were examined and compared to reference marks made from offering plasticine to live animals, as well as marks from tooth imprints of museum specimens. We also set up 24 camera-monitored nests in the forest sites (Trailmaster® Model TM1500 Active Infrared Trail Monitor and TM35-1 Camera Kit) that were separated from nests at the transects by at least 100 m. Cameras were not set up in the rural habitat for security reasons. Twenty baited live rodent traps were randomly placed in each transect and deployed overnight after the experiment proper concluded

to identify and assess the abundance of potential small-mammal predators.

Statistical analyses

To test whether the probability of predation differed among the set-ups, general linear mixed models (GLMM) were fitted to the data. Mixed models can flexibly represent the covariance structure arising from clustered data (Pinheiro & Bates 2000). Each observation of nests or caterpillars predated vs. not predated was coded as the response variable, height and habitat as fixed effects (predictor variables), and transects and plots as nested random effects (control variables) to account for the non-independence in spatial location of set-ups. The GLMMs were fitted using the 'lme4' package in R version 2.2.0 (R Development Core Team; http://cran.r-project.org/), by specifying a logit link function and a binomial error structure for the response. The effect of each predictor variable was first evaluated separately. Collinearity between variables was assessed using the 'perturb' function in the 'Perturb' package, which evaluates changes to the parameter estimates when each predictor variable is randomly reclassified. From a maximal model that included both predictors and their interaction term, a set of candidate models was obtained by sequentially removing the variable/interaction term with the least contribution to model adequacy. The minimal adequate model was selected on the basis of parsimony using the Akaike's Information Criterion (AIC). To determine if vegetation density affected predation, Spearman's rank correlations were performed between the mean predation and measured vegetation variables in each transect.

RESULTS

Nest predation

Overall predation on nests was lowest in the open-canopy forest (16.7%) and highest in the rural areas (58.3%) (Table 1). Predation in the closed-canopy forest was intermediate between the other two habitats (32.8%). Single fixed effect analyses showed that nests in rural areas suffered higher predation than those in closed-canopy forests (estimate = 0.26, P = 0.06) (Table 2). Additionally, nests at 1–1.5 m suffered significantly lower predation than ground nests (estimate = −0.15, P = 0.03) (Table 2). The minimal adequate model for nest predation included habitat, height and their interaction term, suggesting that the effect of habitat type on predation differed among different nest heights (Table 3).

Table 1. Numbers of artificial nests and caterpillar models predated at different habitats and height categories. Predator type was determined from nest remains and bite marks on plasticine (incisor width > 2 mm for large mammals and < 2 mm for small mammals). Set-ups where neither eggs nor caterpillar models were recovered were considered missing/not determined.

	Artificial nests			Caterpillar models		
	Closed canopy	Open canopy	Rural	Closed canopy	Open canopy	Rural
Ground (total)	19	14	43	22	30	43
Missing/not determined	9	3	6	4	2	3
Large mammals	4	2	–	–	–	–
Small mammals	6	7	23	2	–	8
Birds	–	2	11	7	24	31
Reptiles	–	–	2	–	–	1
Arthropods	–	–	–	9	4	–
1–1.5 m (total)	16	6	27	27	28	35
Missing/not determined	6	1	13	2	4	1
Large mammals	9	2	–	–	–	–
Small mammals	1	1	2	1	1	2
Birds	–	2	11	6	17	29
Reptiles	–	–	1	–	–	–
Arthropods	–	–	–	18	6	3
> 5 and > 3 m (total)	24	10	35	34	33	29
Missing/not determined	12	4	31	3	6	3
Large mammals	10	1	–	1	–	–
Small mammals	–	1	1	–	–	–
Birds	2	4	2	6	16	23
Reptiles	–	–	–	–	–	–
Arthropods	–	–	–	24	11	3

Table 2. Single fixed effect models of probability of nest and caterpillar predation (df in both models = 537) with habitat and height as predictors and the inclusion of transect and plot as nested clustering variables to control for spatial autocorrelation.

Fixed effect	Estimate	t	P
Nest predation			
Habitat			
Closed-canopy forest (reference)	–	–	–
Open-canopy forest	−0.16 ± 0.12	−1.33	0.184
Rural areas	0.26 ± 0.13	1.90	0.058
Height			
Ground (reference)	–	–	–
1–1.5 m	−0.15 ± 0.07	−2.20	0.028
> 5 m	−0.04 ± 0.05	−0.82	0.413
Caterpillar predation			
Habitat			
Closed-canopy forest (reference)	–	–	–
Open-canopy forest	0.04 ± 0.11	0.40	0.689
Rural areas	0.13 ± 0.06	2.21	0.027
Height			
Ground (reference)	–	–	–
1–1.5 m	−0.03 ± 0.08	−0.37	0.713
> 3 m	0.01 ± 0.08	0.07	0.943

Caterpillar predation

Predation on the caterpillars had an increasing trend with 46.1%, 50.6% and 59.4% of the models showing

Table 3. Minimal adequate model of probability of nest predation (loglikelihood = −326; df = 531, AIC = 707). The full model included both predictors and their interaction term and transect and plot as nested clustering variables to control for spatial autocorrelation. Model simplification was based on Akaike's Information Criterion.

Fixed effect	Estimate	t	P
Intercept	1.32 ± 0.11	12.0	< 0.001
Habitat			
Closed-canopy forest (reference)	–	–	–
Open-canopy forest	−0.08 ± 0.15	−0.56	0.576
Rural areas	0.40 ± 0.16	2.52	0.012
Height			
Ground (reference)	–	–	–
1–1.5 m	−0.05 ± 0.10	−0.49	0.624
> 5 m	0.08 ± 0.10	0.82	0.414
Habitat × height			
Open-canopy forest × 1–1.5 m	−0.08 ± 0.16	−0.52	0.603
Rural areas × 1–1.5 m	−0.22 ± 0.16	−1.35	0.177
Open-canopy forest × > 5 m	−0.15 ± 0.16	−0.94	0.350
Rural areas × > 5 m	−0.22 ± 0.16	−1.35	0.177

beak or bite marks in the closed-canopy forest, open-canopy forest and rural areas, respectively (Table 1). Single fixed effect analyses showed that caterpillars in rural areas suffered significantly higher predation than those in closed-canopy forests (estimate = 0.13, P = 0.03) (Table 2). The minimal adequate model for caterpillar predation (loglikelihood = −385; df = 537; AIC = 802) included habitat as the sole predictor, since the removal of the other terms did not result in a significant decrease in deviance.

Vegetation variables

Measures of the vegetation variables were significantly different among the three habitats (ANOVA, P < 0.05). Canopy cover and tree density decreased with increasing disturbance, while vegetation at 0–1 m showed the opposite trend. The measured vegetation variables were not significantly correlated with mean predation in the transects for either nests or caterpillars (Spearman's correlation, n = 12, P > 0.05).

Potential predators

The infrared cameras were able to capture three separate predation events by long-tailed macaques, *Macaca fasicularis* (Raffles). Other large-mammal predators (> 2 mm incisor width) were the Philippine warty pig, *Sus philippensis* Nehring, and the common palm civet, *Paradoxurus hemaphroditus* (Pallas). Small-mammal predators (< 2 mm incisor width) were rodents, namely the Oriental house rat, *Rattus tanezumi* Temminck, the

common brown rat, *R. norvegicus* (Berkenhout), the Polynesian rat, *R. exulans* (Peale), and large forest rat, *Bullimus* sp. The potential avian nest predators that were observed were corvids such as the large-billed crow, *Corvus macrorhynchos* Wagler and crested myna, *Acridotheres cristatellus* (Linnaeus). The majority of the attacks on caterpillars were by birds and arthropods (e.g. ants, spiders). Marks by arthropod predators were pooled into one category. Out of 80 trap nights in each habitat, overall trap success was 11.3%, 22.5% and 32.5% for closed-canopy, open-canopy and rural areas, respectively. There were significantly fewer rodents caught by the live traps in the closed-canopy forest than in the other habitats (n = 12, Kruskal–Wallis H = 8.41, df = 2, P < 0.05). However, the number of rodents was not significantly correlated with predation of caterpillars or nests at ground level (n = 12, Spearman correlation P > 0.05).

Predator abundance was found to vary among the three habitat types (Table 1). Out of 194 predated nests, it was not possible to determine predators or recover eggs from 85 (43.8%). Based on the marks on the retrieved models, the closed-canopy forest had higher instances of large-mammal predation. Birds and small mammals were responsible for the majority of the nest predation in the open-canopy and rural areas. A total of 281 caterpillar models was predated upon, 28 (10.0%) of which were not recovered. Bird predation on caterpillars increased with disturbance, while arthropod predation showed the opposite trend. More marks by rodents were also observed in the rural areas, where there was also one incidence of reptile attack (Table 1).

DISCUSSION

Nest predation experiments have been conducted extensively in temperate habitats (Söderström 1999) and although knowledge on predation in the tropics has been growing, South-East Asia remains understudied. Predation is known to vary with the vertical location of nests (Martin 1993a) and we found that ground nests were significantly more predated than nests at 1–1.5 m, supporting previous findings that ground-dwelling birds are more susceptible to nest mortality in the tropics (Söderström 1999). How pressures differ for tree-nesters has not been elucidated, with only a few studies in temperate areas having examined trends at heights greater than 3 m (Ortega *et al.* 1998, Reitsma & Whelan 2000). In this study, nests at heights greater than 5 m had intermediate levels of predation and were mainly attacked by airborne or scansorial predators such as birds and macaques. In contrast, small terrestrial mammals such as rodents were responsible for most losses at ground level (Estrada *et al.* 2002, Gibbs 1991, Sodhi *et al.* 2003, Wong

et al. 1998). Nests at 1–1.5 m were the least predated, so they may be somewhat less conspicuous. Perhaps their intermediate position might make them less accessible to both terrestrial and airborne predators, especially in structurally complex habitats.

Habitat degradation can lead to higher levels of nest predation (Martin 1993b). Of the three habitats, the open-canopy forest had fewer instances of nest predation. This was inconsistent with the expectation that predation would be lowest in the less-disturbed closed-canopy forest. One possible reason for the lower predation is that human disturbance may negatively impact some predators (Gibbs 1991). For instance, predation by large mammals decreased outside of the closed-canopy forest, possibly because *M. fasicularis* avoid or are present in lower densities in areas with higher disturbance. Rural areas had a significantly higher number of predated nests than the forest sites. Previous studies have linked higher rates of predation to habitat openness (Estrada *et al.* 2002, Gibbs 1991, Telleria & Diaz 1995). While we did not find a correlation between our measured vegetation variables and nest predation, we observed an increase of attacks by birds, which are visually oriented predators (Table 1). In contrast to the closed-canopy forest, evidence of attacks by avian predators was found at all three vegetation strata in the rural areas. Small mammals were the other major predators in the rural areas, where they also gained access to higher nests. Previous studies found predation by small mammals to be more common in the tropical forest interior (Cooper & Francis 1998, Telleria & Diaz 1995). However, we found predation events by rodents increased outside the forest. As they are generalist predators, rodents are abundant near farms and human settlements, which provide novel food sources (Angelstam 1986). Thus they may make habitats outside the forest or forest edges adjacent to agriculture unsuitable for nesting, especially for ground-nesters.

The effects of habitat alteration on invertebrate predation rates are even less understood (Koh & Menge 2006). Caterpillar predation was higher in rural areas than in closed-canopy forest, but predation was not significantly different among the three height strata. Predation by birds increased with disturbance (Table 1), which suggests it is more difficult for them to locate prey in the closed-canopy forest. Arthropod predation was highest in the closed-canopy site, although the proportion was lower than in other studies (90% or greater, Koh & Menge 2006, Loiselle & Farji-Brener 2002). Arthropod species richness is generally correlated with plant species richness, vegetation height and complexity (Gaston 1992, Haysom & Coulson 1998). Higher diversity of plants and the presence of higher canopy cover may explain the presence of more invertebrate predators in the forest. In addition, many invertebrates are sensitive to habitat modification (Kremen *et al.* 1993) and the negative effect of disturbance on arthropods may have caused their decline as the dominant predators of caterpillars in the rural areas.

Aside from affecting the assemblage of predators and their ability to locate prey, habitat degradation can cause direct loss of features needed by certain species for reproduction (e.g. reduce the diversity of nest sites) (Martin 1993b). However, quantifying the variables that directly affect predation may continue to be difficult (Sodhi *et al.* 2003). As in other studies in the tropics (Koh & Menge 2006, Wong *et al.* 1998), we did not find any of the measured vegetation variables or even predator abundance to be significantly correlated with predation in the three habitats. The use of artificial models is well known to be subject to many biases (Major & Kendall 1996), and the levels of predation observed cannot be taken to reflect actual losses experienced by real nests and caterpillars. Ideally, natural populations should be monitored to find out if they are negatively affected by increased predation. However, the differences in relative predation pressure and predator assemblages among the habitats in this study show that human disturbance can have marked effects on biotic interactions. To maintain populations of forest fauna, such changes that affect the reproductive success of species must be understood. If altered predation patterns make habitats unsuitable for reproduction, they may become ecological traps (Schlaepfer *et al.* 2002). Future work can evaluate if rural areas, which have been found to retain some biodiversity (Horner-Devine *et al.* 2003, Peh *et al.* 2005, Sodhi *et al.* 2005), indeed act as ecological traps for forest species.

ACKNOWLEDGEMENTS

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