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BIRDS DEFEND OIL PALMS FROM HERBIVOROUS INSECTS

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Abstract. Top-down forces are expected to be important in regulating herbivore populations in most agricultural systems where primary productivity is high and species diversity is low. Under such conditions, trophic cascades are predicted to occur when predator populations are reduced or removed. Studies on how predator removal indirectly affects herbivory rates in agricultural systems are lacking. Through a bird-exclosure experiment, I test the hypothesis that insectivorous birds indirectly defend oil palms (*Elaeis guineensis*) from herbivorous insects. Results show that bird exclusion significantly increased herbivory damage to oil palms, and that the size of this exclusion effect increased with bird density, although the latter result was not statistically significant. These findings suggest that insectivorous birds deliver a natural pest control service for oil palm agriculture, which is important not only for the direct benefits it delivers for human welfare, but also in strengthening the economic justifications for conserving the remaining natural habitats and biodiversity in agricultural landscapes.

Key words: agriculture; biodiversity hotspots; conservation; ecosystem services; natural capital; reconciliation ecology; restoration ecology.

Introduction

One of the central questions in ecology is to understand the degree to which herbivore populations are limited by top-down controls (e.g., predation [Hairston et al. 1960, Lawton and Strong 1981, Terborgh 1988]) vs. bottom-up effects (e.g., resource limitation [Ehrlich and Raven 1965, Polis and Strong 1996]). Most ecologists now agree that the two sets of forces vary in relative importance with respect to space and time (Hunter and Price 1992, Denno et al. 2003, 2005, Gripenberg and Roslin 2007). In most agricultural systems where primary productivity is high (i.e., plant resources are nonlimiting) and species diversity is low (i.e., trophic interactions are simple), top-down forces are expected to be important in regulating herbivore populations (Oksanen et al. 1981, Schmitz 1992, Strong 1992). Under such conditions, trophic cascades are predicted to occur when predator populations are reduced or removed, resulting in increased herbivore populations and herbivory damage to crops (Paine 1966, 1980). Understanding the role of natural enemies in providing such pest control services is important not only for the direct benefits it delivers for human welfare, but also in strengthening the economic justifications for conserving the remaining natural habitats and biodiversity in agricultural landscapes (Matson et al. 1997, Naylor and Ehrlich 1997, Daily et al. 2000, Balvanera et al. 2001, Daily and Ellison 2002, Sekercioglu et al. 2004). However, apart from a few notable exceptions (e.g., Greenberg et al. 2000, Mols and Visser 2002), studies on how predator removal indirectly affects herbivory rates in agricultural systems are lacking, particularly from tropical regions.

The oil palm (*Elaeis guineensis*) is one of the most rapidly expanding crops in the tropics (Koh 2007*a*, *b*, Koh and Wilcove 2007). Like most monocultures, oil palm suffers from attacks by a variety of insect pests (see Plate 1). Severe pest outbreaks occasionally occur causing massive defoliation, which results in substantial yield reductions and financial costs to oil palm companies (Wood et al. 1973, Corley and Tinker 2003). Most companies now adopt an integrated pest management approach, which favors the use of non-chemical pest control methods, such as the establishment of "beneficial plants" (e.g., *Euphorbia heterophylla*) to attract the insect predators and parasitoids of oil palm pests (e.g., the wasp, *Dolichogenidea metesae* [Basri et al. 1995, Corley and Tinker 2003]). Recent studies reveal that oil palm plantations can support a commu-

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PLATE 1. The caterpillar, *Setora nitens*, is one of several leaf-eating lepidopteran pests of oil palm agriculture in Southeast Asia (Corley and Tinker 2003). Photo credit: L. P. Koh.

nity of birds, a majority of which prey on insects (Desmier de Chenon and Susanto 2005, Koh 2007*a*). The potential contribution of birds to the control of insect pests in oil palm agriculture has not been quantified. In this study, I investigate whether insectivorous birds indirectly defend oil palm foliage from herbivorous insects. Through a bird-exclosure experiment, I test the predictions that (a) oil palms in bird-exclosure treatments (inaccessible to birds) experience higher herbivory rates than oil palms in control treatments (accessible to birds); and (b) the effect size of excluding birds (i.e., ratio of the herbivory rate in the bird-exclosure treatment to that in the paired control treatment) increases with the population density of insectivorous birds.

METHODS

This study was conducted in an oil palm complex (4°27.561′ N ,18°13.953′ E; comprising ∼19 000 ha of oil palm plantations) in East Sabah, Malaysia, located on the island of Borneo in Southeast Asia. In a previous study, I recorded the species richness and population density of birds in this oil palm complex (Koh 2007*a*). In that study, birds were sampled in standard-length (100-m) transects that were located randomly and at least 1 km apart. During days of fair weather (i.e., no rain or overcast sky), transects were walked between 06:00 and 10:00 hours at a constant pace and with a pause for a 1-min visual census at every 10-m interval. Every unique bird individual spotted or heard 50 m to each side, 50 m ahead, and 50 m above was recorded once. Eight of the previously surveyed transects, which varied in bird density (Appendix), were selected as experimental plots to test the predictions of this study. This experiment was conducted between 14 May and 5 June 2007.

Oil palm seedlings of approximately uniform age (∼1 year old) and height (∼1 m) were obtained from a nursery located in the oil palm complex. All chemical treatments (e.g., pesticides) on these seedlings were stopped one week prior to the start of the experiment. At this age, each oil palm seedling possesses ∼8–10 leaves, each leaf comprising ∼20–30 leaflets. For each seedling, I randomly selected 20 leaflets that had perfect and undamaged laminae, and marked the base of each leaflet with a waterproof marker pen. Seedling herbivory rates were quantified at the end of the experiment based on the extent of pest damage observed on these marked leaflets. Three seedlings were placed ∼10 m apart at each of the eight experimental plots. Each seedling represented a different experimental treatment: a bird-exclosure treatment, a control treatment, and a "sham" treatment (procedural control). The bird-exclosure treatment, which comprised a wire cage measuring ∼100 × 100 × 120 cm (length × breadth × height) and had a mesh size of ∼2.5 × 2.5 cm, was placed over a seedling. This treatment allowed potential insect pests access to the seedling, while excluding all insectivorous birds. The smallest insectivorous bird species recorded (Koh 2007*a*) from the experimental plots was *Orthotomus ruficeps* (beak-to-tail length of 11 cm [MacKinnon and Phillipps 1993]). The control treatment consisted of a seedling that remained uncaged and exposed to both birds and insects. For the sham treatment, a rectangular piece of the cage material (∼50 × 30 cm) was erected adjacent (∼15 cm) to an uncaged seedling. This procedural

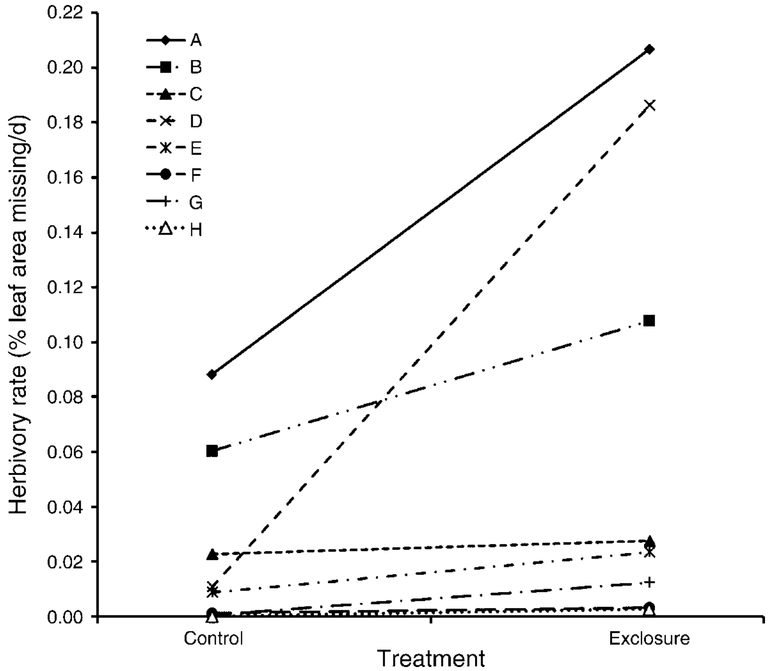

FIG. 1. Effects of bird exclusion on rate of herbivory on oil palm (*Elaeis guineensis*) seedlings for each of the eight replicates of the exclusion experiment. Each replicate comprises a pair of control and exclosure treatments (A–H).

control was used to test whether the cage material had an effect on oil palm herbivory rates. At the end of the experiment, every marked leaflet from the seedlings was collected and digitally photographed. The area of laminae missing from each leaflet was calculated using Adobe Photoshop CS2 (Adobe Systems Incorporated, San Jose, California, USA). Oil palm seedlings were exposed to treatment for 21 or 22 days. The herbivory rate for each seedling was quantified as the average proportion of laminae area missing per leaflet per day the seedling remained in the field. A total of eight leaflets were not recovered (representing 1.7% of total sample size) and were excluded from subsequent analyses. Throughout the duration of the study, experimental plots were regularly visited to ensure that cages were not disturbed by humans or animals. Nonetheless, one of the sham cages was toppled, and it was excluded from subsequent analyses.

To maximize statistical power given the loss of one sham treatment, I performed two paired-sample t tests to test distinct hypotheses: (a) that the cage material did not attract herbivores (i.e., there was no significant difference in herbivory rates between sham and control treatments); and (b) bird exclusion had no effect on herbivory damage on oil palms (i.e., there was no significant difference in herbivory rates between control and bird-exclosure treatments). To determine the relationship between the effect size of bird exclusion and bird density, I fitted a linear regression model to the data by specifying the population density of insectivorous birds as the predictor variable and the effect size of bird exclusion as the response variable. To satisfy the assumptions of normality, the angular transformation (arcsine square-root transformed) was applied to each variable of herbivory rate, and the natural-log transformation was applied to the variable of effect size prior to the analyses. All statistical tests were performed using R (R Development Core Team 2007).

RESULTS

Herbivory rates in sham treatments (0.042% $\pm$ 0.022% per day; mean $\pm$ SE) and control treatments (0.024% $\pm$ 0.012% per day) were not significantly different ($t = 0.87$, df = 6, $P = 0.418$), suggesting that the cage material did not attract herbivorous insects. Herbivory rates in bird-exclosure treatments (0.071% $\pm$ 0.030% per day) were significantly higher than that in control treatments ($t = 2.658$, df = 7, $P = 0.033$ [Fig. 1]). Where birds were excluded from oil palm seedlings, herbivory rates increased by between 1.2- and 17.2-fold. The fitted linear regression model, which has a slope of 0.156 $\pm$ 0.087 and an intercept of 0.199 $\pm$ 0.773, shows that the effect size of bird exclusion increased with the population density of insectivorous birds, although this trend was not statistically significant ($R^2 = 35.2\%$, df = 6, $P = 0.121$ [Fig. 2]).

DISCUSSION

My results suggest that insectivorous birds provide important ecosystem services in agricultural systems and function as predicted in basic food chain models (Paine 1966, 1980). The exclusion of insectivorous birds from

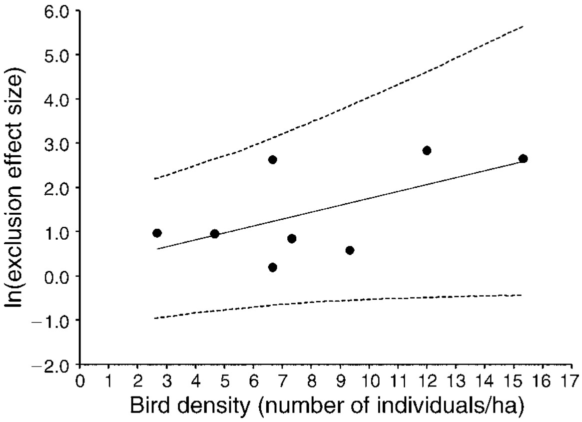

FIG. 2. Plot of the ln-transformed effect size of bird exclusion against the population density of insectivorous birds. Effect size is calculated as the ratio of the herbivory rate in the bird-exclosure treatment to that in the paired control treatment. The solid line represents the predicted values of effect sizes based on a linear regression model fitted to the data, which has a slope of 0.156 ± 0.087 (mean ± SE) and an intercept of 0.199 ± 0.773; dashed lines represent bootstrapped 95% upper and lower confidence limits based on 10 000 iterations.

oil palm seedlings resulted in an average increase in herbivory rate of 0.047% per day. Assuming that this effect applies equally to mature oil palms, the removal of bird predators from oil palm plantations could result in ~28% foliage damage over the effective life span of an oil palm leaf (~600 days, taking conventional leaf pruning rates into account [Corley and Tinker 2003]). Wood et al. (1973) conducted a manual defoliation experiment on oil palms and reported that a 25% loss of foliage resulted in fruit yield losses of between 9% and 26% in the first year after defoliation. These results suggest that insectivorous birds could be providing an economically valuable pest control service for oil palm agriculture.

A recent study shows that insectivorous birds in oil palm plantations such as *Centropus sinensis*, *Copsychus saularis*, *Orthotomus ruficeps*, and *Pycnonotus goiavier* likely prey on common oil palm pests such as *Setora nitens*, *Metisa plana*, and *Segestes* spp. (Desmier de Chenon and Susanto 2005). This suggests that insectivorous birds likely function as important pest control agents for oil palm agriculture. Studies in other agricultural systems reveal similar conclusions. For example, Great Tits (*Parus major*) were shown to be effective in reducing both pest caterpillar numbers and fruit damage in apple orchards (*Malus domestica*) (Mols and Visser 2002). In Guatemalan coffee plantations (*Coffea arabica*), Greenberg et al. (2000) report a significant increase in the frequency of herbivore damage in bird-exclosure treatments compared to control treatments.

Oil palm herbivory rates were higher by between 1.2- and 17.2-fold in bird-exclosure than in control treatments. A possible explanation for this variation in the effect size of bird exclusion is that birds may become ineffective at controlling pest populations where bird densities are low (Tinbergen 1960). My results reveal a positive, albeit nonsignificant, relationship between the density of insectivorous birds and exclusion effect size, which is consistent with this hypothesis. The statistical nonsignificance of this trend may be due in part to the small sample size of the experiment ($n = 8$). An alternative explanation for the variation in exclusion effect size is that birds may become ineffective at controlling pest populations where pest densities exceed a threshold level (Otvos 1979).

Although I used an experimental approach, two caveats are relevant. The first caveat is that insectivory by predators other than birds (e.g., bats) could have contributed to the observed effects of predator exclusion. Also, because the density of potential insect pests had not been quantified, the experimental results may be open to alternative interpretations. However, my finding that the density of insectivorous birds explained 35.2% of the variation in the effect size of predator exclusion supports the hypothesis that insectivorous birds play an important role in defending oil palms from insect pests. A second caveat of this study is that because seedlings were used in the experiment instead of mature palms, its results may have limited applicability to mature oil palm plantations.

Oil palm plantation managers would benefit by modifying local vegetation characteristics to maintain insectivorous birds. Ground and epiphytic ferns (e.g., *Nephrolepsis biserrata*) may provide nesting sites for several insectivorous birds such as *Orthotomus ruficeps*, *Pycnonotus goiavier* and *Prinia flaviventris* (Desmier de Chenon and Susanto 2005). The prevalence of epiphytes on palm trees and the amount of ground vegetation cover have also been shown to have positive effects on the diversity of birds in oil palm plantations (Koh 2007*a*). These findings suggest that the modification of local vegetation characteristics could make oil palm plantations more hospitable for birds and thereby help maintain the natural pest control services they provide for oil palm agriculture, which could reduce the need for traditional chemical methods. This would not only avoid the damaging effects of pesticides to both plantation workers and the environment, but also satisfy the growing consumer preference for oil palm products produced through environmentally friendly practices (Koh and Wilcove 2007). The preservation of natural habitats is important for oil palm biodiversity and should be incorporated into the development of better management practices in oil palm agriculture. This would maximize the benefits derived from pest control services delivered by birds and other predators.

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APPENDIX

A table containing a species list of insectivorous birds recorded from the study site, and a table showing abundance, population density, and species richness of insectivorous birds in each of the eight experimental plots (*Ecological Archives* A018-026-A1).