ECOLOGICAL AND ECONOMIC SERVICES PROVIDED BY BIRDS ON
JAMAICAN BLUE MOUNTAIN COFFEE FARMS

By

Jherime L. Kellermann

A Thesis

Presented to

The Faculty of Humboldt State University

In Partial Fulfillment

Of the Requirements for the Degree

Master of Science

In Natural Resources: Wildlife

(May, 2007)

ECOLOGICAL AND ECONOMIC SERVICES PROVIDED BY BIRDS ON
JAMAICAN BLUE MOUNTAIN COFFEE FARMS

By

Jherime L. Kellermann

Approved by the Master's Thesis Committee:

Dr. Matthew D. Johnson, Major Professor	Date
Dr. Mark A. Colwell, Committee Member	Date
Dr. T. Luke George, Committee Member	Date
Dr. Gary Hendrickson, Graduate Coordinator	Date
Dona E. Shafer, Dean for Research and Graduate Studies	Date

ABSTRACT

ECOLOGICAL AND ECONOMIC SERVICES PROVIDED BY BIRDS ON JAMAICAN BLUE MOUNTAIN COFFEE FARMS

Jherime L. Kellermann

Coffee farms can support significant biodiversity, yet intensification of farming practices is degrading agricultural habitats, compromising ecosystem services such as biological pest control. The Coffee Berry-borer, *Hypothenemus hampei* is the world's primary coffee pest. Studies indicate that birds can reduce insect abundance on coffee farms, although no research has examined avian control of berry-borer or quantified avian benefits to crop yield or farm income. I conducted a bird exclosure experiment on four coffee farms in the Blue Mountains, Jamaica to document avian pest control of berry-borer, identify potential avian predator species, associate predator abundance and berry-borer reductions with habitat complexity, and economically quantify resulting yield increases. Coffee plants excluded from foraging birds had significantly greater infestation, more broods, and greater berry damage than paired control plants. We identified 17 predator species; 67% of detections were wintering Neotropical migrants, and three primary species comprised 50% of these. Migrant predators overall did not respond to vegetation complexity while primary predators increased with proximity to habitat patches. Resident predator species increased with shade-tree cover and coffee shrub density. Berry-borer reductions were not correlated with predator abundance or vegetation complexity. The market value of increased berries from pest reductions was

U.S. \$44-\$105 per hectare for 2005/2006. High regional landscape heterogeneity may allow primary predators to provide pest control broadly, despite localized farming intensities, but further agricultural intensification could disrupt current services. These results provide the first evidence that birds control berry-borer, increasing coffee yield and farm income, a potentially important conservation incentive for producers.

ACKNOWLEDGMENTS

I would like to thank my advisor, Dr. Matthew Johnson and my committee, Drs. Mark Colwell and Luke George, and the additional support and consultation of Drs. Dwight Robinson, Steve Hackett, Mike Mesler, and Bill Bigg. Special thanks to Amy M. Stercho for her hard work throughout the project. Additional field assistance was provided by Rob Fowler, Damian "Rooster" Whyte, Roger, and Lynden. The project would not have been possible without the cooperation of the farmers; Dorian Campbell, Don McGraham, Jacqui Sharpe, Richard Sharpe, and Wallenford Coffee Company. Funding was provided by American Museum of Natural History, Cooper Ornithological Society, Humboldt State University, National Geographic Society, and U.S. Fish and Wildlife Service. Additional technical support came from the Jamaican Conservation and Development Trust and the University of the West Indies. Thanks to my lab mates Rebecca Green, Amy Liest, Amy Roberts, Jim Tietz, Chris Tonra, and Eric Wood.

TABLE OF CONTENTS

	Page
ABSTRACT.....	iii
ACKNOWLEDGMENTS	v
LIST OF TABLES.....	viii
LIST OF FIGURES	ix
INTRODUCTION	1
METHODS	4
Study Sites	4
Bird Exclosures.....	5
Coffee Berry-borer Surveys.....	6
Bird Surveys	7
Vegetation Complexity.....	8
Ecological Analyses.....	9
Economic Analysis	11
RESULTS	12
Coffee berry-borer	12
Avian Predators	16
Vegetation Complexity	19
Economic Value.....	19
DISCUSSION	21
Ecosystem services provided by birds	21

Mobile predators and landscape heterogeneity.....	24
Economic value	25
REFERENCES	27

LIST OF TABLES

Table	Page
1	Bird species identified as potential Coffee Berry-borer predators on coffee farms in the Blue Mountains, Jamaica. I calculated the average percent shade, and distance to nearest habitat patch for each species by averaging the measured vegetation values of the 400 m ² plots in which each detection occurred for all detections of the species.....18
2	Economic benefit of birds in U.S. dollars (USD) per hectare (ha) calculated for four Jamaican Blue Mountain coffee farms during the 2005/2006 production year ($\pm$ 95% confidence interval).....20

LIST OF FIGURES

Figure	Page
1 Mean ($\pm$ 1SE) proportion of coffee berries infested with coffee berry-borer from exclosure plants (black) and control plants (gray) over 5 survey periods from November 2005/January 2006 to April/May 2006, Jamaica.....	14
2 Mean ($\pm$ 1SE) depth of Coffee Berry-borer penetration in berries with and without broods from coffee plants inside exclosures and control plants.....	15

INTRODUCTION

A vast and expanding percentage of terrestrial habitats are altered for human settlement and commodity production. Effective biodiversity conservation must not focus only on pristine habitats, but also include the array of matrix components comprising fragmented landscapes (Pimentel et al. 1992, Ricketts 2001). Complex agricultural ecosystems in particular are capable of supporting significant species richness (Daily 1997, Altieri 1999), but many of these are threatened by modern agricultural practices. Recognition of specific ecosystem processes and components present in traditional, biologically diverse agroecosystems that enable and sustain production of economically important goods could provide effective conservation incentives, especially in developing tropical countries (Gatzweiler 2006).

Coffee (*Coffea arabica* and *C. robusta*) is the second-most traded global commodity by developing nations after oil (Rice 1999). With global production based in the tropics, coffee farms are important components of biogeographically diverse regions (Stattersfield et al. 1998, Moguel and Toledo 1999) and strategic targets for conservation. If properly managed, structurally and biologically complex coffee farms can provide habitat for a variety of taxa (Ibarra-Nunez 1990; Perfecto et al. 1996; Greenberg et al. 1997; Wunderle and Latta 1998; Mas and Dietsch 2004). In the 1970s, coffee varieties that thrive in direct sun were developed to increase production (Dietsch et al. 2004). The subsequent intensification of coffee cultivation has resulted in ecological simplification, which directly compromises biodiversity via loss of species, habitat, and their associated

ecosystem services (Perfecto et al. 1996; Naylor and Ehrlich 1997; Perfecto and Vandermeer 2002). In particular, agricultural intensification of coffee and other crops has reduced the integrity and viability of natural biological pest control through the loss of predator species (Tscharntke et al. 2005).

The world's predominant coffee pest is the Coffee Berry-borer, *Hypothenemus hampei* (Coleoptera: Scolytidae) (Damon 2000; Chavez and Riley 2001). Nearly the entire life cycle of the species takes place inside the coffee berry: Gravid females bore galleries into the fruit's endosperm where they lay their eggs, the brood develops over 28 to 34 days, nourished by the endosperm (Damon 2000); mature females then mate exclusively with their flightless male siblings who rarely leave the berry, emerge gravid from the fruit in 23-28 days, and immediately seek out a new coffee berry for oviposition (Brun et al. 1995). Berry-borer infestation results in economic losses to coffee producers through direct declines in yield and quality and further vulnerability of infested fruit to disease, fungus and other pests (Damon 2000).

A number of biological controls for berry-borer have been examined (Chavez and Riley 2001; Poinar et al. 2004), with mixed implementation and economic success (Bachelor et al. 2005). Introduced parasitoid wasps have been somewhat effective in Mexico and Central America, however, the parasitoids die out when pest populations become sparse and must be re-introduced (Damon 2000; Castillo et al. 2004). Despite studies showing birds to effectively control agricultural insect pests in temperate regions (Tremblay et al. 2001; Mols and Visser 2002), reduce arthropods of several taxonomic groups in Guatemalan (Greenberg et al. 2000) and Puerto Rican coffee farms

(Borkhataria et al. 2006), and suppress simulated outbreaks of Lepidopteran caterpillars in Mexican coffee farms (Perfecto et al. 2004), no research has yet examined the reduction of Coffee Berry-borer by birds or provided direct evidence that these effects benefit crop production or farm income. Additionally, birds and their services have been shown to increase with the complexity of vegetative cover in coffee farms (Wunderle and Latta 1998; Greenberg et al. 2000; Perfecto et al. 2004). Linking increases of saleable coffee berries associated with reductions in berry-borer by native insectivorous birds could provide a strong economic incentive to coffee farmers to conserve habitat for birds and other biodiversity.

I conducted a bird exclosure experiment on coffee farms in the Blue Mountains of Jamaica, West Indies to examine the ecological and economic pest control services provided by birds. My goals were to 1) measure reductions by birds of berry-borer, berry-borer broods, and coffee berry damage, 2) identify potential avian predator species of berry-borer and determine if their abundances increase with greater vegetation complexity, 3) determine if greater pest reductions are associated with greater bird abundance and vegetation complexity, and 4) quantify the economic value of any observed pest reductions due to birds by calculating increases of saleable coffee berries.

METHODS

Study Sites

Jamaica, the third largest island in the Greater Antillean Archipelago, is 11,400 km², with approximately 10,000 hectares devoted to coffee agriculture (Luntta 1997). After 200 years of traditional shade-grown production, coffee berry-borer was inadvertently introduced to Jamaica in 1978 (Robinson and Mansingh 1999). The Blue Mountains of Jamaica yield some of the world's most expensive and celebrated coffee (Robinson and Mansingh 1999); with roasted beans bringing up to U.S. \$80 per pound on the Japanese market.

I selected four farms in the Blue Mountains located within a roughly 10 km² area and a 500 m elevational band. All farms bordered the Blue and John Crow Mountains National Park, represented a range in structural complexity and agricultural intensification within and between farms, grew *Coffea arabica* var. *tipica*, and were willing to participate in the project for at least one year. Wallenford farm contained 22 ha of coffee in intensive "full-sun" cultivation. Clifton Mount farm had 34 ha of coffee grown under a range of vegetation complexity. McGraham farm contained 6 ha of coffee with agricultural practices similar to Clifton Mount. McGraham retained trees for erosion control, but were heavily pruned to limit shade. Rowan's Royal farm had 0.6 ha of certified organic coffee with a complex and diverse vegetation structure typical of small-scale polycultural shade-coffee production in Jamaica. Annual pesticide

application on the three non-organic farms occurred four months prior to the commencement of my study, and was not performed again until after project completion.

Bird Exclosures

To measure reductions of berry-borer, brood abundance, and berry damage by birds on individual coffee plants, I randomly selected coffee plant pairs stratified across the four study farms ($n = 30$). The experimental plant of each pair received a bird-proof exclosure while the other plant remained available to bird predation and served as a control for paired comparisons. I selected experimental coffee plants by mapping farm borders and generating random points that were at least 10 meters from the farm edge and 10 meters apart using ArcView 3.3. The plant nearest to the random point that was 1.5 to 2.5 m tall and flowering or bearing fruit was selected as the experimental plant receiving the bird exclosure. A control plant used for paired comparisons was the nearest plant within 1-5 meters of the experimental plant but not touching and was visually assessed to be most similar in height, width, branch, stem, and leaf density, and level of flowering and/or fruiting. Exclosures on Wallenford ($n = 10$) and Rowan's Royal ($n = 5$) were built in late November 2005; exclosures on Clifton Mount ($n = 10$) and McGraham ($n = 5$) were built in early January 2006. Our construction of exclosures coincided with the emergence of ripe fruit on each farm.

I constructed exclosures using a pyramidal-style pole frame over individual coffee plants. The frames were composed of roughly 5 m long saplings or bamboo collected locally. The frame was wrapped in a single length of transparent nylon gill netting

(N163A 58 mm mesh, Nylon Net Co., Memphis TN, USA), tied shut with twine and the bottom staked into the ground to prevent entry of ground foraging birds. The large 58mm netting of the bird exclosures did not appear to restrict access by *Anolis* lizards, butterflies, bees or other invertebrates, which would require smaller grade mesh material (Borkhartaria et al. 2006).

Coffee Berry-borer Surveys

To determine coffee berry-borer infestation levels on each plant of all experimental plant pairs ($n = 30$), I inspected 100 berries per plant and recorded the proportion of infested berries. Berries were chosen systematically across the plant, from available berries. Irregular fruiting of coffee plants meant that often, some portions of individual plants would not have any fruit while others would be heavily laden. Therefore, I distributed my counts as evenly as possible across the available fruits on all vertical and lateral portions of the plant, never counting more than two fruits within a single “cluster” of fruits. I sampled fruits of all sizes and levels of ripeness and inspected berries for borer entry holes, which were almost exclusively initiated at the top of the ovary. I measured initial berry-borer infestation levels at the time of exclosure construction for both exclosure and control plants. I subsequently visited all plant pairs the first week of every month from January through May 2006 and report berry-borer survey time as the number of months since exclosure construction. Exclosure and control proportions of berry-borer infestation were square-root transformed to meet normality assumptions.

I harvested all ripe berries from the plant pairs, maintaining the harvest schedule of each farm. To determine berry-borer brood presence and extent of berry damage I dissected all harvested berries infested with borer. I used the depth of borer penetration into the berry (distance from point of entry to the most distal bored area in mm) as a measure of berry damage. During berry dissection, I recorded the presence or absence of a brood at any life cycle stage. Prior to dissection I tested the "float" of every infested berry, a post-harvest technique used by farmers in the field to separate damaged or malformed fruits, which float in water and are discarded. Depth of penetration was natural log transformed for analysis.

Bird Surveys

I performed 20-minute surveys of foraging birds within a 400 m² plot centered on each enclosure to identify bird species potentially responsible for observed reductions of berry-borer infestation. I alternated periods of stationary observation and slow walking to observe all portions of the plot and to gain sufficient views of birds in the plot. I surveyed each plot once a month from February through April between sunrise and 10:00 (CST) on the same day as berry-borer surveys. For each individual bird in the plot, I recorded the vertical vegetation layer it occupied (tree, coffee, ground) during the first foraging bout (if any) initiated after detection. Birds flying through or over the plot without foraging were not recorded.

Bird species that were observed foraging within coffee shrubs on one or more occasions and at least occasionally ingest tiny invertebrates ($\leq 3\text{mm}$, Lack 1976) were

considered potential berry-borer predators. For analyses, I used average total number of birds, bird species, and berry-borer predators per plot from February through April as response variables. All bird variables were square-root transformed to meet normality assumptions.

Vegetation Complexity

Within the 400 m² foraging plots ($n = 30$), I measured percent shade cover (see below), number of coffee plants (≥ 1 m), number of banana plants (≥ 1 m), and number, average height, and average diameter at breast height (dbh) of shade trees. I used two methods of measuring shade. Using a densiometer (Forestry Suppliers Inc. Jackson, MS, USA), which measures vegetative cover directly overhead, I averaged five readings, one at the north side of the enclosure and one at each cardinal direction 5 m from the enclosure, to determine a shade value for each plot. I also used a solar pathfinder (Solar Pathfinder, Linden, TN, USA), to measure total annual solar insulation/percent shade at a site at each enclosure and control plant, which I averaged to characterize each plot. I used a Geographic Positioning System (Garmin Ltd, Olathe, KS) to determine elevation of each enclosure.

I also visually estimated the linear distance from each plant pair ($n = 30$) to the nearest tree, habitat patch, and farm edge vegetation within a ninety-degree arc centered on each cardinal bearing, which could extend beyond the 400 m² plot boundary. I defined a tree as any woody, non-coffee plant >5 m tall and a habitat patch as an area ≥ 10 m² of woody non-coffee vegetation with elements >5 m tall, both of which birds can use

as “stepping stones” to move through areas (Wunderle 1999). From these distances I created six variables for each plant pair: the single nearest distance to each of the three vegetation components from any one direction (nearest tree, patch, edge) and the average distance to each component across all four directions (average tree, patch, edge). Nearest tree, patch, and edge were square-root transformed and average distance to tree was natural log transformed to meet normality assumptions. Average patch and edge did not require transformations.

Ecological Analyses

To determine if birds significantly reduced coffee berry-borer infestation, I compared infestation levels between exclosure and control plant treatments with one-tailed paired-t tests for each of the five survey periods, using an adjusted alpha (0.01) for performing five comparisons (Gotelli and Ellison 2004). When infestation proportions over the entire five month study period are pooled, the data set contained a large proportion of zeros resulting in a strongly skewed distribution. Therefore, I opted for five separate parametric tests where the monthly proportions could be normalized with square root transformations. However, these tests are not independent and results should be approached with some caution.

I used chi-square analysis to compare the number of infested berries with berry-borer broods from exclosure and control plants. To examine damage of coffee berries from berry-borer infestation, I analyzed the difference in depth of borer penetration

between infested berries from exclosure and control plants and between berries that floated or sank in water with one-tailed t-tests for equal variance.

Several of the vegetation measures I collected represent different manners of sampling the same habitat characteristic (e.g. percent shade and number of trees). To avoid including collinear variables in regression models (Legendre and Legendre 1998) I entered all four dependent bird variables, the berry-borer reduction dependent variable (see results) and all 13 independent vegetation variables into a Spearman-Rank correlation matrix (Greaves et al. 2006). To create a subset of independent variables, I first chose the variable with the highest Spearman-Rank correlation coefficient for all dependent variables, and then eliminated all independent variables that were collinear ($r > 0.60$) with the selected variable (Beck and George 2000). I repeated this process with the remaining variables until I established a subset of non-collinear independent variables. I then entered these remaining variables into forward stepwise regression ($\alpha = 0.15$ to enter) to further select from the subset of independent vegetation variables (Anderson et al. 2000). I used multiple regression to relate the final selected vegetation complexity variables with each dependent variable. All analyses were run in SPSS 13.0 (2004).

Economic Analysis

I conducted interviews with managers from each farm to determine the number of acres of coffee in production, number of boxes of coffee produced per acre, and price received per box. To estimate the economic value to coffee farmers of reduced crop damage due to bird predation, I first quantified each farm's average proportional yield increase in saleable berries resulting from coffee berry-borer reductions due to bird predation (Δ_{CBB}) by subtracting the monthly berry-borer infestation level of each control plant from its paired exclosure plant and then calculating the average reduction on each farm across surveys two through four (Fig. 1). This value was translated into an economic benefit of birds to each farm for the 2005-2006 production season using the formula

$$\Delta_{CBB} \times \frac{\#boxes}{ha} \times \frac{US\$}{box} \times acres,$$

where a box refers to a standard 27.2 kg unit of coffee berry harvest used in Jamaica. I calculated 95% confidence limits for berry-borer reduction (mean $\pm [t_{df,0.05} \times \text{Standard Error}]$) and then used them to calculate the confidence intervals for benefit per hectare, farm, and total study area.

RESULTS

Coffee berry-borer

Berry-borer reductions ranged from 1% to 14% for individual plant pairs. For all plants combined at the time of exclosure construction (survey 0), control plants had significantly higher mean proportions of coffee berry-borer infestation than exclosures ($t = 2.86$, $df = 28$, $p < 0.004$, Fig. 1). One month later (survey 1), exclosure plants free from bird predation had developed higher levels than controls, although not significantly ($t = 1.06$, $df = 28$, $p = 0.29$, Fig. 1). By survey 2, exclosure plants had attained significantly higher berry-borer infestation levels than controls ($t = 3.20$, $df = 27$, $p < 0.002$) and this was maintained during survey 3 ($t = 3.28$, $df = 24$, $p < 0.002$) and survey 4 ($t = 2.8$, $df = 19$, $p = 0.006$) (Fig. 1).

One outlying pair of plants at Wallenford farm was excluded from these analyses because its infestation levels were two to five times greater than any other plant in the study, potentially due to its location adjacent to an area of unpruned coffee that was allowed to grow twice the height typical for the farm and may have harbored high pest levels; its control plant had normal berry-borer levels. My sample size was also reduced across the survey periods as coffee plants ended their fruiting cycle, no longer providing sufficient berries for surveys.

I dissected 224 ripe coffee berries infested with berry-borer. Berries from plants inside exclosures contained significantly more broods (38 of 111) than control fruits (20 of 113) ($\chi^2 = 8.63$, $df = 1$, $p = 0.003$) and were bored deeper (mean $\pm$ SE = 5.48 ± 0.32 mm) than controls (3.87 ± 0.25 mm; $t = 3.76$, $df = 222$, $p < 0.001$; Fig. 2). Depth of penetration remained significantly greater in exclosure berries ($n = 73$, mean = 3.68 ± 0.24 mm) than control berries ($n = 93$, mean = 2.94 ± 0.18 mm; $t = 2.22$, $df = 164$, $p = 0.014$; Fig. 2) after removing the berries containing broods from analysis, which restricted the comparison to damage done by the adult female boring into the berry. Berries that floated were bored deeper (mean = 5.56 ± 0.46 mm) than those that did not float (mean = 4.29 ± 0.22 mm; $t = 2.20$, $df = 222$, $p = 0.014$).

Figure 1. Mean (± 1 SE) proportion of coffee berries infested with coffee berry-borer from exclusion plants (black) and control plants (gray) over 5 survey periods from November 2005/January 2006 to April/May 2006, Jamaica.

Figure 2. Mean ($\pm$ 1SE) depth of Coffee Berry-borer penetration in berries with and without broods from coffee plants inside exclosures and control plants.

Avian Predators

I made 354 bird detections of 43 bird species during 112 foraging surveys (Table 1), with 57% of all detections in coffee, 33% in trees, 6% on the ground, and 4% in non-coffee shrubs. I observed 23 species foraging at least once in coffee. Based on diet criteria, I considered 17 species to be potential berry-borer predators (Table 1). Twelve of these 17 were *Parulid* warblers, with 11 North American migrants and the Jamaican endemic, *D. pharetra*. In addition to the endemic today, there were two endemic vireos, Blue Mountain Vireo *Vireo osburni* and Jamaican Vireo *Vireo modestus*, the Black-whiskered Vireo *Vireo altiloquus*, a breeding resident, and the Banaquit *Coereba flaveola*, a year-round resident. Neotropical migratory warblers represented over 73% of all predator detections and nearly 67% of those were of just three species: *D. caerulescens*, *S. ruticilla*, and *D. discolor*. Because (1) migrant and resident bird species can show different habitat associations (Wunderle 1999), (2) these three warbler species are common winter residents throughout much of the Greater Antilles (Holmes et al. 1989, Wunderle 1999, Wunderle & Latta 2000, Latta and Faaborg 2001), and (3) I had over two to four times more detections of these species than the next most common migrant (Table 1), I made an *ad hoc* split of the total predators variable into three new variables for subsequent analyses; migrant predators, resident predators, and primary predators, which includes the top three migrant predator species.

Initial variable selection resulted in a subset of five vegetation variables for inclusion in subsequent multivariate analyses; shade (densiometer), number of coffee

shrubs, number of banana trees, distance to nearest habitat patch, and average distance to farm edge. Average number of total birds ($R^2 = 0.37$, $F_{1,28} = 16.62$, $p = 0.0003$) and number of species ($R^2 = 0.42$, $F_{1,28} = 20.1$, $p < 0.0001$) increased significantly with increasing percent shade cover. Migrant predators were not significantly associated with any vegetation variables, while resident predators showed a positive significant correlation with shade ($R^2 = 0.35$, $F_{1,28} = 14.9$, $p < 0.001$). In contrast, primary predators increased with decreasing distance to the nearest habitat patch ($R^2 = 0.14$, $F_{1,28} = 4.61$, $p = 0.04$).

Table 1. Bird species identified as potential Coffee Berry-borer predators on coffee farms in the Blue Mountains, Jamaica. I calculated the average percent shade, and distance to nearest habitat patch for each species by averaging the measured vegetation values of the 400 m² plots in which each detection occurred for all detections of the species.

Species		Total predator detection s	% of total detection s	% Shade tree cover	Nearest habitat patch (m)
Black-throated Blue Warbler	<i>Dendroica caerulescens</i>	43	24	31	17
American Redstart	<i>Setophaga ruticilla</i>	24	13	23	21
Prairie Warbler	<i>Dendroica discolor</i>	22	12	18	29
Arrowhead Warbler	<i>Dendroica pharetra</i>	14	8	51	11
Jamaican Tody	<i>Todus todus</i>	11	6	32	17
Common Yellowthroat	<i>Geothlypis trichas</i>	10	6	31	15
Yellow-rumped Warbler	<i>Dendroica coronata</i>	10	6	7	18
Banaquit	<i>Coereba flaveola</i>	9	5	36	15
Ovenbird	<i>Seiurus aurocapillus</i>	8	4	35	12
Palm Warbler	<i>Dendroica palmarum</i>	8	4	9	29
Black-whiskered Vireo	<i>Vireo altiloquus</i>	7	4	60	9
Jamaican Vireo	<i>Vireo modestus</i>	5	3	68	10
Black-and-white Warbler	<i>Mniotilta varia</i>	4	2	75	3
Blue Mountain Vireo	<i>Vireo osburni</i>	2	1	56	0
Northern Parula	<i>Parula americana</i>	2	1	0	46
Swainson's Warbler	<i>Limnothlypis swainsonii</i>	1	1	31	0
Tennessee Warbler	<i>Vermivora peregrina</i>	1	1	31	0

Vegetation Complexity

I averaged berry-borer reduction for each experimental plant pair across surveys with significantly greater infestation of exclosure plants (2-4, Figure 1). Reduction was not associated with any measures of vegetation complexity included in the variable subset, or with elevation ($R^2 = 0.04$, $F_{1,27} = 1.02$, $p = 0.3$), which ranged from 864 m to 1316 m. Average berry-borer showed a significant positive correlation with average total bird species ($R^2 = 0.25$, $F_{1,28} = 9.21$, $p = 0.005$) and average total birds ($R^2 = 0.21$, $F_{1,28} = 7.31$, $p = 0.011$) but was not correlated with any predator species variables.

Economic Value

All four farms received the same regional standard price for the 2005/2006 season of U.S. \$48 per box of coffee berries. Coffee plant damage caused by hurricane Ivan in 2004 decreased yields, thus coffee buyers paid producers a higher compensatory price during my study period. The value of pest control services of birds to farmers in terms of increased volume of saleable berries during this stage of production ranged from U.S. \$44 to \$105 per ha (Table 2). Summed across the entire 62.6 ha of our study area, the total economic value of increased coffee crop yield due to bird predation was U.S. \$4,018 $\pm$ 2,805 (95% confidence interval).

Table 2. Economic benefit of birds in U.S. dollars (USD) per hectare (ha) calculated for four Jamaican Blue Mountain coffee farms during the 2005/2006 production year ($\pm 95\%$ confidence interval).

Farm	ha mature coffee	boxes/ha	Berry-borer reduction	USD/box	USD benefit of birds/ha	USD benefit of birds/Farm
Rowan's Royale	0.6	82	0.026 ± 0.020	48	102 ± 79	62 ± 48
Clifton Mount	34	77	0.012 ± 0.006	48	44 ± 24	1440 ± 775
McGraham	6	85	0.013 ± 0.012	48	52 ± 37	171 ± 119
Wallenford	22	91	0.024 ± 0.019	48	105 ± 84	2344 ± 1863

DISCUSSION

Ecosystem services provided by birds

Birds supplied ecologically and economically valuable services to Blue Mountain Coffee farmers in Jamaica, providing the first evidence that birds can directly benefit coffee yield and farm income via pest control. In this experiment, avian predators reduced adult berry-borer infestation, number of berry-borer broods, and extent of berry damage. These services likely result from avian predation of adult female berry-borer as they search for an oviposition site or bore into the endosperm, which can take up to eight hours (Damon 2000; J. K., personal observation). During much of that time, berry-borers may be reliable and easily detectable prey for insectivorous birds that consume small arthropods. The deeper penetration of berries in exclosures suggests that birds continue to depredate berry-borer even after they have commenced boring into the berry.

We assert that the pest control services detected in this experiment were due to bird predation and were not attributable to other factors. Although we were unable to directly observe birds predating berry-borer, on a coffee farm in another region of Jamaica 53%, 56%, and 44% of diet samples obtained from Black-throated Blue Warblers, American Redstarts, and Prairie Warblers respectively contained coffee berry-borer (M. Johnson & T. Sherry unpublished data). Data for other species are not available. Furthermore, we regularly observed small *Anolis* lizards, another important arthropod predator (Borkhataria et al. 2006), inside exclosures and on control plants. Access by other insects, such as parasitoid wasps that attack berry-borer (Damon 2000)

and pollinators that can affect coffee's fruit set (Ricketts et al. 2004), were also unlikely to be restricted by 58 mm mesh. Temperature and relative humidity recorded by data loggers (HOBO Pro v2, Bourne, MA) on one plant pair at each farm over eight hours were nearly identical for exclosure and control plants, regardless of weather conditions (M. J. & J. K., unpublished data).

The decline of borer infestation on control plants over the first two months of the study coincides with the arrival of Neotropical migrants from North America, which nearly double Jamaica's summer population (Lack 1976). Migrants constituted more than 60% of all birds detected on our survey plots. Despite the prevalence of wintering migrants, resident species may also provide significant pest control. Arrowhead Warbler and Jamaican Tody comprised 14% of total predator detections and nearly 60% of resident predator detections (Table 1). Average resident predator abundance and average bird abundance and diversity increased significantly with greater shade cover (Table 1). Farms with greater vegetation heterogeneity and thus greater functional diversity of avian predator species could exhibit stronger resilience of services after disturbances such as hurricanes through "insurance" species (Loreau et al. 2003; Tscharntke et al. 2005). Avian ecosystem services may be particularly vulnerable to intensive habitat degradation and fragmentation due to the high trophic level of birds (Dobson et al. 2006) and the sensitivity of avian insectivores (Şekercioğlu et al. 2002) and Neotropical migratory species to population decline (Maurer & Haywood 1993). Research on winter territory size, habitat associations, and the movement of resident and wintering migratory predator species within and between farms and bordering habitats is needed to better understand

the relationship between landscape complexity, habitat simplification, and the provision of pest control services.

The difference in berry-borer infestation between farms may reflect differential pesticide use. Rowan's Royale, the only certified organic coffee farm in Jamaica (D. Robinson, personal communication), had significantly higher infestation inside enclosures (mean = 0.185) than all other farms combined (0.123, $F_{1,128} = 7.29$, $p < 0.01$). However, mean infestation of control plants where birds were foraging was equivalent on Rowan's Royale (0.118) and non-organic farms (0.101, $F_{1,128} = 0.68$, $p < 0.41$), suggesting the profitability of berry-borer as prey for birds may be density dependent. Pesticides, applied 4 months before our data collection, may initially reduce berry-borer infestation, but bird predation appears to reduce and/or maintain levels to around 10% on both organic and conventional farms throughout the remainder of the season. Due to higher ambient infestation on the organic farm, more berry-borers were removed to reach these levels. Interestingly, extreme inbreeding of berry-borer may foster rapid genetic resistance to Endosulphan (Brun et al. 1995), which could reduce its impacts in the Blue Mountains, where it has been used since 1978 (Robinson & Mansingh 1997).

Temperature and humidity also influence berry-borer abundance (Damon 2000). The relatively small reductions (1-14%) we detected on experimental plants may reflect the cool, wet conditions typical of Blue Mountain farms (D. Robinson, personal communication). During preliminary experiments, we found reductions of 11% to 38% one month after the exclusion of birds under much hotter and drier conditions of a lower elevation farm (625 m, J. K., unpublished data). Additional experimental research on

avian pest control of berry-borer should be conducted across a range of biogeographic regions and alongside other pest control methods to better inform integrated pest management and conservation strategies.

Mobile predators and landscape heterogeneity

If birds reduce berry-borer and increase with vegetation complexity, why did we not find corresponding reductions of berry-borer? Mobile agents such as birds can provide ecosystem services to areas beyond their primary habitats (Kremen 2007). In particular, migratory warblers, which comprised 73% of all predator detections, utilize a wide variety of habitats with varying disturbance regimes on their wintering grounds in the West Indies (Holmes et al. 1989; Wunderle & Waide 1993; Confer & Holmes 1995; Johnson & Sherry 2001; Latta & Faaborg 2001, Sillett & Holmes 2002, Johnson et al. 2006). Detections of the three primary predator species on plots declined only after a distance of 40 to 50 meters from habitat patches (Fig. 3), while average distance across the entire study area was only 40 m. The comparatively small size of the farms (0.6 to 34 ha) and the diversity of neighboring land parcels may dilute negative effects of intense agricultural practices via these bird species (Altieri 1999). The Blue Mountain matrix likely provides sufficient habitat in the form of parks, forest fragments, riparian strips, fallow pasture, and rural gardens for primary predators to exploit interspersed patches of intensive “sun-coffee” and possibly include them in their winter home ranges (Wunderle & Latta 1998; Latta & Faaborg 2001). Although intensively managed areas are currently benefiting from local landscape diversity, continued degradation could lead to regional

deterioration of ecosystem services (Şekercioğlu et al. 2004). Further research in regions with geographically extensive agricultural intensification is urgently needed to determine at what level these ecosystem services may become significantly reduced or eliminated.

Our assessment of vegetation complexity did not consider species composition or diversity, a significant factor in avian presence and utilization of coffee farms (Perfecto et al. 2004). The farms in our study region mostly utilized native tree species for shade cover such as Blue Mahoe *Hibiscus elatus* and Dovewood *Alchornea latifolia* mixed with some non-native species including Caribbean Pine *Pinus caribbea* and mango *Mangifera spp.* In order to optimize the attractiveness of a farm to beneficial birds, species composition of the planned and unplanned crop and non-crop biodiversity on farms should be considered (Perfecto & Vandermeer 2002).

Economic value

Our simple economic model based on the difference in the proportion of berries infested by berry-borer between exclosure and control plants estimated an average benefit of U.S. \$75/ha (Table 2). The economic significance of avian services becomes more apparent when considering Jamaica's per capita GNI of U.S. \$3,400 in 2005 (World Bank 2006). Pest control services were equivalent to 2% to 69% of the per capita GNI for the lowest to highest production farms respectively (Table 2).

These values represent the benefit to only four farms in the Blue Mountains of Jamaica, totaling U.S. \$4,018 (118% of the per capita GNI) for the 2005/2006 season. Our analyses do not take into account other associated benefits of bird predation, such as

reduced pesticide applications or the reduction of other pests. Economic benefits may be far greater on farms at lower elevations or in warmer, drier regions where berry-borer abundances can be much higher. Furthermore, we quantified the value of increases in saleable beans to coffee producers only. The increasing value of coffee could be considered as it is traded from producers to processors and wholesalers, and ultimately to retailers and consumers. All of these substantial economic benefits are dependant on the natural capital of the region (Costanza et al. 1997), specifically, the heterogeneous habitats that sustain viable wintering populations of Neotropical migratory warblers and resident species of Jamaican avifauna that provide these valuable ecosystem services.

REFERENCES

- Altieri, M. A. 1999. The ecological role of biodiversity in agroecosystems. *Agriculture, Ecosystems and Environment* 74: 19-31.
- Anderson, D. R., K. P. Burnham, and W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* 64: 912-923.
- Batchelor, T. P., I. C. W. Hardy, J. F. Barrera, and G. Perez-Lachaud. 2005. Insect gladiators II: Competitive interactions within and between bethylid parasitoid species of the coffee berry borer, *Hypothenemus hampei* (Coleoptera:Scolytidae). *Biological Control* 33: 194-202.
- Beck, M. J. and T. L. George. 2000. Song post and foraging site characteristics of breeding Varied Thrushes in Northwestern California. *Condor* 102: 93-103.
- Borkhataria, R. R., J. A. Collazo, and M. J. Groom. 2006. Additive effects of vertebrate predators on insects in a Puerto Rican coffee plantation. *Ecological Applications* 16: 696-703.
- Brun, L. O., J. Stuart, V. Gaudichon, K. Aronstein, and R.H. French-Constant. 1995. Functional haplodiploidy: a mechanism for the spread of insecticide resistance in an important insect pest. *Proceedings of the National Academy of Science* 92: 9861-9865.
- Castillo, A., F. Infante, and J. F. Barrera. 2002. First field report of a nematode (Tylenchida: Sphaerularioidae) attacking the coffee berry borer, *Hypothenemus hampei* (Ferrari) (Coleoptera:Scolytidae) in the Americas. *Journal of Invertebrate Pathology* 79: 199-202.
- Chavez, B. and J. Riley. 2001. Determination of factors influencing integrated pest Management adoption in coffee berry borer in Colombian farms. *Agriculture, Ecosystems and Environment* 87: 159-177.
- Confer, J. L. and R. T. Holmes. 1995. Neotropical migrants in undisturbed and human altered forests of Jamaica. *The Wilson Bulletin* 107: 577-589.
- Costanza, R., R. d'Arge, R. de Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naem, R. O'Neill, J. Paruelo, R. Raskin, P. Sutton, and M. van den Belt. 1997. The Value of the World's Ecosystem Services and Natural Capital. *Nature* 387: 253-260.

- Daily, G. C. 1997. Introduction: what are ecosystem services. pp. 1-10 *In* Nature's Services: societal dependence on natural ecosystems G. C. Daily ed. Island Press, Covelo, California.
- Damon, A. 2000. A review of the biology and control of the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Scolytidae). Bulletin of Entomological Research 90: 453-465
- Dietsch, T. V., S. M. Philpott, R. A. Rice, R. Greenberg, and P. Bichier. 2004. Conservation Policy in coffee landscapes. Science 303: 625.
- Dobson, A., D. Lodge, J. Alder, G. S. Cummings, J. Keymer, J. McGlade, H. Mooney, J. A. Rusak, O. Sala, V. Walters, D. Wall, R. Winfree, and M. A. Xenopoulos. 2006. Habitat loss, trophic collapse, and the decline of ecosystems services. Ecology 87: 1915-1924.
- Gatzweiler, F. W. 2006. Organizing a public ecosystem service economy for sustaining biodiversity. Ecological Economics 59: 296-304.
- Gotelli, N. J. and A. M. Ellison. 2004. A primer of Ecological Statistics. Sinauer Associates, Inc., Sunderland, Massachusetts.
- Greaves, R. K., R. A. Sanderson, and S. P. Rushton. 2006. Predicting species occurrence using information-theoretic approaches and significance testing: An example of dormouse distribution in Cumbria, UK. Biological Conservation 130: 239-250.
- Greenberg, R., P. Bichier, A. C. Angon, C. MacVean, R. Perez, and E. Cano. 2000. The impact of avian insectivory on arthropods and leaf damage in Guatemalan coffee plantations. Ecology 81: 1750-1755.
- Holmes, R. T., T. W. Sherry, and L. Reitsma. 1989. Population structure, territoriality and overwinter survival of two migrant warbler species in Jamaica. Condor 91: 545-561.
- Ibarra-Nunez, G. 1990. Los arthropodos asociados a cefetos en un cafetal mixto del Soconusco, Chiapas, Mexico. Folia Entomologica Mexicana 79: 207-231.
- Johnson, M. D. and T. W. Sherry. 2001. Effects of food availability on the distribution of migratory warblers among habitats in Jamaica. Journal of Animal Ecology 70: 546-560.

- Johnson, M. D., T. W. Sherry, R.T. Holmes, and P. P. Marra. 2006. Assessing Habitat Quality for a migratory songbird in natural and agricultural habitats. *Conservation Biology* 20: 1433-1444.
- Kremen, C., N. M. Williams, M. A. Aizen, B. Gemmill-Herren, G. LeBuhn, R. Minckley, L. Packer, S. G. Potts, T. Roulston, I. Steffan-Dewenter, D. P. Va'zquez, R. Winfree, L. Adams, E. E. Crone, S. S. Greenleaf, T. H. Keitt, A. Klein, J. Regetz, and T. H. Ricketts. 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters* 10: 299-314.
- Lack, D. 1976. *Island Biology: Illustrated by the landbirds of Jamaica*. University of California Press, Berkeley, California.
- Latta, S. C. and J. Faaborg. 2001. Winter site fidelity of Prairie Warblers in the Dominican Republic. *Condor* 103: 455-468.
- Legendre, P., and L. Legendre. 1998. *Numerical Ecology Developments in Environmental Modeling*, vol. 20. Elsevier, Amsterdam.
- Loreau, M., N. Mouquet, and A. Gonzales. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Science* 100: 12765-12770.
- Luntta, K. 1997. Coffee heaven in Jamaica. *Boston Globe Sunday*, November 23, pp. M1.
- Manley, F. J., L. McDonald, and D. L. Thomas. 2002. *Resource selection by animals: statistical design and analysis for field studies*, 2nd edition. Chapman and Hall Publishers, London.
- Mas, A. H. and T. V. Dietsch. 2004. Linking shade coffee certification to biodiversity conservation: Butterflies and birds in Chiapas, Mexico. *Ecological Applications* 14: 642-654.
- Maurer, B. A. and S. G. Haywood. 1993. Geographic range fragmentation and abundance in Neotropical migratory birds. *Conservation Biology* 7(3): 501-509.
- Moguel P. and V. M. Toledo. 1999. Biodiversity Conservation in traditional coffee systems Of Mexico. *Conservation Biology* 13: 11-21.
- Mols, C. M. and M. E. Visser. 2002. Great tits can reduce caterpillar damage in apple orchards. *Journal of Applied Ecology* 39: 888-899.

- Naylor, R. L., and P. R. Ehrlich. 1997. Natural pest control services and agriculture. 151-176 *In* Nature's Services: societal dependence on natural ecosystems G. C. Daily ed. Island Press, Covelo, California.
- Perfecto, I., R. A. Rice, R. Greenberg, and M. E. Van Der Woort. 1996. Shade coffee: a Disappearing refuge for biodiversity. *Bioscience* 46: 598-608. Perfecto, I., and J. Vandermeer. 2002. Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. *Conservation Biology* 16: 174-182
- Perfecto, I., J. Vandermeer, G. Bautista, G. Nunez, R. Greenberg, P. Bichier, and S. Langridge. 2004. Greater predation in shaded coffee farms: The role of resident neotropical birds. *Ecology* 85: 2677-2681.
- Pimentel, D., U. Stachow, D. A. Takacs, H. W. Brubaker, A. R. Dumas, J. J. Meaney, J. A. S. O'Neil, D. E. Onsi, and D. B. Corzilius. 1992. Conserving biological diversity in agricultural-forestry systems: most biological diversity exists in human-managed ecosystems. *Bio-Science* 42: 354-362.
- Poinar, G., F. E. Vega, A. Castillo, I. E. Chavez, and F. Infante. 2004. *Metaparasitylenchus hypothenemin* sp. (Nematoda: Allantnematidae), a parasite of the coffee berry borer, *Hypothenemus hampei* (Curculionidae: Scolytinae). *Journal of Parasitology* 90(5): 1106-1110.
- Ricketts, T. H. 2001. The matrix matters: Effective isolation in fragmented landscapes. *American Naturalist* 158: 87-99.
- Ricketts, T. H., G. C. Daily, P. R. Ehrlich, and C. D. Michener. 2004. Economic value of forest to coffee production. *Proceedings of the National Academy of Science* 101: 12579-12582.
- Rice, R. A. 1999. A place unbecoming: the coffee farm or Northern Latin America. *Geographical Review* 89:554-579.
- Robinson, D. E. and A. Mansingh. 1999. Insecticide contamination of the Jamaican Environment. IV. Transport of residues from coffee plantations in the Blue Mountains to coastal waters in Eastern Jamaica. *Environmental Monitoring and Assessment* 54: 125-141.
- Şekercioğlu, C., P. R. Ehrlich, G. C. Daily, D. Aygen, D. Goehring, and R. F. Sandi. 2002. Disappearance of insectivorous birds from tropical forest fragments. *Proceedings of the National Academy of Science* 99: 263-267.
- Şekercioğlu, C., G. C. Daily, and P. R. Ehrlich. 2004. Ecosystem consequences of bird declines. *Proceedings of the National Academy of Science* 101: 18042-18047.

- Sillett, T. S. and R. T. Holmes. 2001. Variation in survivorship of a migratory songbird throughout its annual cycle. *Journal of Animal Ecology* 71: 296-308.
- Stattersfield, A., M. Crosby, A., Long, and D. Wege. 1998. *Endemic Bird Areas of the World: Priorities for Biodiversity Conservation*. BirdLife International, Cambridge.
- Tremblay, A., P. Mineau, and R. K. Stewart. 2001. Effects of bird's predation on some pest insect populations in corn. *Agriculture, Ecosystems and Environment* 83: 143-152.
- Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity ecosystem service management. *Ecology Letters* 8: 857-874.
- World Bank. 2006. <http://web.worldbank.org>
- Wunderle, J. M. and R.B. Waide. 1993. Distribution of overwintering Nearctic migrants in the Bahamas and Greater Antilles. *Condor* 95: 904-933.
- Wunderle, J. M. and S. C. Latta. 1998. Avian resource use in Dominican shade coffee plantations. *Wilson Bulletin* 110: 271-281.
- Wunderle, J. M. 1999. Avian distribution in Dominican shade coffee plantations: Area and habitat relationships. *Journal of Field Ornithology* 70: 58-70