

THE BEHAVIOR AND ECOLOGY OF BIRDS IN TROPICAL FOREST RESTORATION  
SITES.

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## ABSTRACT

### THE BEHAVIOR AND ECOLOGY OF BIRDS IN TROPICAL FOREST RESTORATION SITES.

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Forest restoration has become an important management tool that facilitates forest regeneration. However there has been little study thus far that examines how well restored plots, and particular planting designs, function over time in providing suitable habitat for tropical animals.

I examined the effects of restoration patch size on the foraging behavior of four resident tropical bird species. I also measure arthropod abundance and anti-predator vigilance behavior to assess whether variation in food availability or predation risk could explain patch size effects on foraging behavior. Prey attack rates were highest, and the effort required to find prey lowest, in larger patches for three of the four bird species. Arthropod density was approximately twice as great in larger patches compared to smaller patches. Evidence for patch size differences in predation risk was more limited but risk may be higher in smaller patches. The results indicate that food availability is the primary mechanism driving patch size effects on foraging behavior.

I compared the habitat quality of the active restoration sites with passive restoration sites, by measuring vegetation structure, arthropod biomass and the foraging behavior of three resident bird species. Although vegetation measures such as amount of understory cover and tree species richness and density differed between the two restoration strategies, arthropod biomass and foraging behavioral measures were

similar. Results suggest that, while active and passive restoration strategies may lead to different vegetation structure, they may support similar biomass of foliage-dwelling arthropods and be similarly used by foraging insectivorous birds.

I also examined the effects of predator vocalizations (direct cues) on the vigilance behavior of birds foraging in different locations: small patches and the center and edges of large patches (indirect cues). Within feeder location, the time birds spent alert increased significantly after a predator compared to a non-predator (control) vocalization in all three locations. However, pairwise comparisons across feeder location showed that the change in time spent alert in response to the predator call was significantly greater in small patches and the edges of large patches compared to the center of large patches. Results show that birds perceive small patches and potentially, the edges of large patches as more risky habitats than the center of large patches. Birds responded more strongly to the direct cue of predation risk when foraging in these locations by increasing vigilance.

I then used an exclosure experiment to examine the top-down effects of birds and bats on arthropods and herbivory. Arthropod biomass was highest on tree branches where both birds and bats were excluded and lowest on branches without exclosures where both birds and bats were present. However, birds and bats had equal impacts on arthropod populations. The size of restoration patches had no significant effect on the impact of birds and bats on arthropod biomass, but did affect levels of leaf damage. These results suggest that both birds and bats play important roles as top-predators in restoration systems by reducing herbivorous arthropods and their damage to planted trees.

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## GENERAL INTRODUCTION

Conversion of forests to pastures for cattle grazing and other agriculture has created large areas of deforested and degraded land in the humid tropics (FAO 2005). Developing effective strategies to restore these lands is critical because of their high biodiversity and their significant role in processes such as water and carbon cycles (Brown 1993). Forest restoration has become an important management tool that facilitates forest regeneration by buffering microclimates in replanted areas, shading out fast-growing grasses and making key nutrients available (Kus 1998, Holl 1999). However there has been little study thus far that examines how well restored plots, and particular planting designs, function over time in providing suitable habitat for tropical animals, whose presence and activities are often key to successful ecosystem recovery.

Animals are important contributors to forest regeneration processes, for example as pollinators (Feldman 2006), seed dispersers (Wunderle 1997) and consumers of herbivorous insects (Van Beal et al. 2003). However, most studies that consider animals in evaluations of restoration success measure species presence/absence and calculate diversity indices (Ruiz-Jaen and Aide 2005). Although valuable, such measures do not provide information about the factors that influence why animals use some sites rather than others. In contrast, behavior patterns demonstrate the importance of particular resources for species (Persson and Stenberg 2006), are strongly linked to fitness (Alcock 2005) and indicate why some habitats are preferred over others (Pomara et al. 2003). Such behavioral studies are important but underutilized tools in the evaluation of restoration success (Lindell 2008).

Many studies have shown that a bird's use of a habitat is sensitive to landscape features (Freemark et al. 1995), patch size (Lee et al. 2000; Zarette et al. 2000) and the availability of specific tree species or foraging substrates (Holmes and Robinson 1981; Parrish 1995; Whelan 2001). One proximate explanation for variation in avian habitat use is that these levels of habitat structure can interact to mediate the abundance and availability of arthropod prey (Wiens et al. 1987; Whelan 1989; Johnson and Sherry 2001). Forest structure, plant species composition (Raman et al. 1998) and prey abundance are inter-related components of a forest habitat quality (Hutto 1990) that affect foraging behavior. The availability of food in a habitat can influence foraging opportunities and foraging behavior in insectivorous birds.

While prey availability can significantly influence avian foraging behavior, other factors such as predation risk may limit an individual's ability to forage in an optimal way. To maximize energy gain, individuals should forage in habitat that provides high food density (Nonacs 2001) and minimizes predation risk (Olsson et al. 2002). Predation risk may be influenced by habitat characteristics such as canopy cover, patch size, and amount of edge (Murcia 1995; Whelan and Maina 2005). In poor quality habitats where predation risk is high, the trade-off between time spent alert for predators and time spent foraging may have significant negative fitness consequences.

Birds and other top predators, especially bats, in tropical systems have the potential to impact other components of tropical restoration systems. Both of these predators consume large quantities of arthropods, many of which are herbivorous and potentially cause damage to vegetation (Marquis and Whelan 1994; Kalko and Kalka 2006). Insectivorous birds and bats could have significant direct effects on herbivorous

arthropod communities and resulting leaf damage to plants (Williams-Guillen et al. 2008; Kalko et al. 2008). Leaf damage due to herbivorous arthropods can negatively affect the growth and survival of tropical plants (Norghauer et al. 2006; Eichorn et al. 2010). Tree seedling survival and growth are critical to the success of tropical forest restoration efforts (Holl et al. 2000), so arthropod predators could play an important role in controlling leaf damage due to herbivory.

My research was conducted in a replicated tropical forest restoration experiment in southern Costa Rica. Sixteen restoration sites were planted between 2004-2006 with four tree seedling species: I used two experimental treatments at each site. Treatment plots were 50 x 50 m and either had (1) trees planted in rows to cover the entire plot (extra-large patch, 2500 m<sup>2</sup>), or (2) trees planted in six patches of three different sizes: two small (16 m<sup>2</sup>), two medium (64 m<sup>2</sup>) and two large patches (144 m<sup>2</sup>).

My research used this replicated restoration project to investigate (1) the effect of restoration patch size on foraging behavioral measures such as prey attack rate and prey search effort, and whether food abundance or predation risk were influencing the variation in foraging behavior among patch sizes, (2) differences avian foraging behavior between active restoration sites and naturally regenerating sites, (3) the effects of direct and indirect cues of predation risk on vigilance in birds foraging in the restoration sites, and (4) the top-down effects of birds and bats on arthropod biomass and leaf damage due to arthropod herbivory in the restoration sites.

## OVERVIEW OF CHAPTERS

In Chapter 1, I examine the effects of restoration patch size on the foraging behavior of four resident tropical bird species. I also measure arthropod abundance and anti-predator vigilance behavior to assess whether variation in food availability or predation risk could explain patch size effects on foraging behavior. Prey attack rates were highest, and the effort required to find prey lowest, in larger patches for three of the four bird species. Arthropod density was approximately twice as great in larger patches ( $> 3500 \text{ m}^2$ ) compared to smaller patches ( $< 350 \text{ m}^2$ ). Evidence for patch size differences in predation risk was more limited but risk may be higher in smaller patches. The results indicate that food availability is the primary mechanism driving patch size effects on foraging behavior, with predation risk being an additional influence for some species in some years. As demonstrated in this study, patches of tens to a few hundreds of metres squared are likely to provide fewer food resources and potentially less cover from predators for vertebrates that use woody habitat, compared to patches of a few thousand metres squared. The more limited resources in smaller patches are likely to have short-term and, potentially, long-term consequences for the fitness of organisms. When considering restoration project design, the potential economic and other benefits of planting in smaller patches must be weighed with the potentially negative ecological effects on some taxonomic groups.

Results from Chapter 1 show that using behavioral measures can reveal what habitat factors are important for birds in restoration systems. Behavioral measures can also be used to compare different types of restoration approaches. Active and passive restoration are two important strategies to aid the recovery of large areas of deforested and degraded tropical lands. Active restoration is where management techniques such

as planting seeds or seedlings are implemented, and passive restoration is when no action is taken except to cease environmental stressors such as agriculture or grazing (Rey Benayas et al. 2008).

In Chapter 2, I compare the habitat quality of the active restoration sites described above, with passive restoration sites, by measuring vegetation structure, arthropod biomass and the foraging behavior of three resident bird species. Both restoration sites had similar land-use histories and times since abandonment. Although vegetation measures such as amount of understory cover and tree species richness and density differed between the two restoration strategies, arthropod biomass and foraging behavioral measures were similar. Results suggest that, while active and passive restoration strategies may lead to different vegetation structure, they may support similar biomass of foliage-dwelling arthropods and be similarly used by foraging insectivorous birds. Passive restoration is generally less costly than active restoration and, if local and landscape characteristics do not impede recovery, may be a viable alternative from the perspective of birds using the sites.

Results from Chapter 1 suggested that predation risk varies among patch size for birds. I explore this idea further in Chapter 3. I examine the effects of predator vocalizations (direct cues) on the vigilance behavior of birds foraging in different locations: small patches and the center and edges of large patches (indirect cues). Within feeder location, the time birds spent alert increased significantly after a predator compared to a non-predator (control) vocalization in all three locations. However, pairwise comparisons across feeder location showed that the change in time spent alert in response to the predator call was significantly greater in small patches and the edges

of large patches compared to the center of large patches. For birds foraging in small patches, the frequency of lateral head turns and duration of head-up bouts increased significantly after the predator compared to the non-predator vocalization. Additionally, the change in head-turn frequency and head-up duration in response to the predator call was significantly greater in small patches compared to the center of large patches. Results show that birds perceive small patches and potentially, the edges of large patches as more risky habitats than the center of large patches. Birds responded more strongly to the direct cue of predation risk when foraging in these locations by increasing a number of vigilance behaviors. These results highlight the importance of investigating avian behavioral responses to the characteristics of restoration sites, many of which consist of small patches of habitat.

My research in Chapters 1-3 demonstrates that the quality of restoration sites can significantly affect the behaviors of birds using the sites. However, birds, and also bats, are themselves likely to impact other components of the restoration system including herbivorous arthropods and the extent of their damage to vegetation (Williams-Guillen et al. 2008; Kalko et al. 2008). The influence of birds and bats on arthropod populations and their indirect effects on leaf damage have not previously been investigated in tropical restoration sites. In Chapter 4, I use an enclosure experiment to examine the top-down effects of birds and bats on arthropods and herbivory. Arthropod biomass was highest on tree branches where both birds and bats were excluded and lowest on branches without enclosures where both birds and bats were present. However, birds and bats had equal impacts on arthropod populations, in contrast to other studies which have found that one or the other predator has stronger

effects on arthropods. The size of restoration patches had no significant effect on the impact of birds and bats on arthropod biomass, but did affect levels of leaf damage. In large patches, levels of leaf damage were higher on branches where birds and bats were excluded than on branches where both had access, but in small patches, no significant differences in herbivory between exclosure treatments were found. These results suggest that both birds and bats play important roles as top-predators in restoration systems by reducing herbivorous arthropods and their damage to planted trees. Tropical restoration projects should include efforts to attract and provide suitable habitat for birds and bats, given their demonstrated ecological importance.

Throughout the rest of this dissertation, I use the term "we" instead of "I", which reflects the true collaborative nature of my work and the fact that all chapters were prepared in manuscript format.



## CHAPTER 1

### PATCH SIZE EFFECTS ON AVIAN FORAGING BEHAVIOR: IMPLICATIONS FOR TROPICAL FOREST RESTORATION DESIGN

#### INTRODUCTION

Tropical forest cover is disappearing at a rapid pace. More than seven million hectares of tropical forest were lost between 2000 and 2005, primarily because of direct conversion of forest to agricultural land covers (FAO 2005). Active restoration, by planting native vegetation, has gained momentum globally and contributed to the reduction in net loss of forest area in many countries (FAO 2005; Chazdon 2008). Developing effective tropical forest restoration strategies will increase the value of restoration efforts and increase the rate at which habitats regenerate (Lamb et al. 2005).

Planting woody vegetation over large areas is an effective restoration technique but is also costly (Parrotta and Engel 2001; Rey Benayas et al. 2008). Planting seedlings in small patches of tens to a few hundred metres squared has been suggested as a potentially cost-effective alternative although this restoration strategy has not been widely implemented nor rigorously tested in comparison with other methods, until very recently (Zahawi and Augspurger 2006; Rey Benayas et al. 2008). Planting small blocks of vegetation mimics the natural regeneration process of 'nucleation', where early successional vegetation establishes patchily and patches coalesce over time (Yarranton and Morrison 1974). This strategy could reduce the cost of restoration by reducing the amount of vegetation planted. However, patch size then becomes an important consideration of restoration design because it may influence the attractiveness of restoration sites to animals. For example, the rate and duration of bird

visits was greater in larger restoration patches in previous studies (Zahawi and Augspurger 2006; Fink et al. 2009). However no previous work has examined why some patch sizes are more attractive to animals than others.

Animals are important contributors to forest regeneration processes, for example as pollinators (Feldman 2006), seed dispersers (Wunderle 1997) and consumers of herbivorous insects (Van Beal et al. 2003). However, most studies that consider animals in evaluations of restoration success measure species presence/absence and calculate diversity indices (Ruiz-Jaen and Aide 2005). Although valuable, such measures do not provide information about the factors that influence why animals use some sites rather than others. In contrast, behaviour patterns demonstrate the importance of particular resources for species (Persson and Stenberg 2006), are strongly linked to fitness (Alcock 2005) and indicate why some habitats are preferred over others (Pomara et al. 2003). Such behavioral studies are important but underutilized tools in the evaluation of restoration success (Lindell 2008).

Foraging behavior measures, such as prey attack rate (number of attacks on prey per unit time) and search effort (locomotor movements per attack) are probably influenced by patch size through food availability (Burke and Nol 1998) and predation risk (Butler et al. 2005). Studies across a variety of spatial scales show that larger patches have greater densities of arthropods (Bach 1988; Burke and Nol 1998; Zanette et al. 2000). Predation risk may be higher in small habitat patches because they offer less cover from predators (Suhonen 1993; Kotler et al. 2004). When predation risk is high, animals increase the proportion of time spent vigilant, negatively affecting foraging efficiency (Caraco et al. 1980; Elgar 1989).

In this study, we examined the effect of restoration patch size on the foraging behavior of four tropical resident bird species in a replicated forest restoration experiment in southern Costa Rica. We tested the hypothesis that patch size influences the foraging behavior of birds and that this effect is due to differences in arthropod abundance and predation risk. We predicted that prey attack rates would be highest and prey search effort lowest in the larger patches because arthropod abundance would be higher (Burke and Nol 1998) and predation risk lower in larger patches (Suhonen 1993).

## METHODS

### *Study Site*

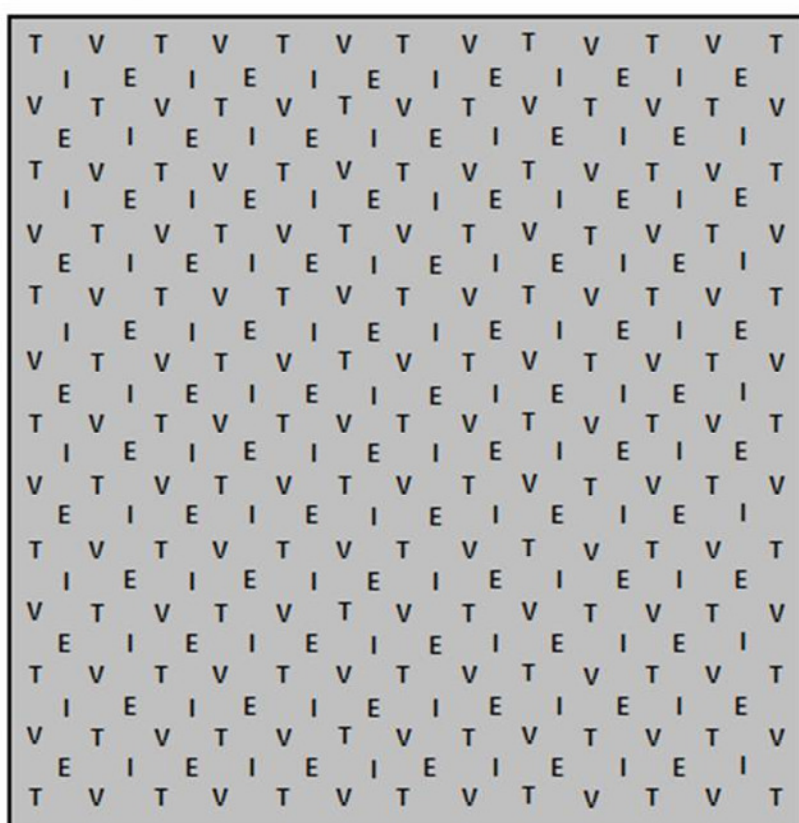
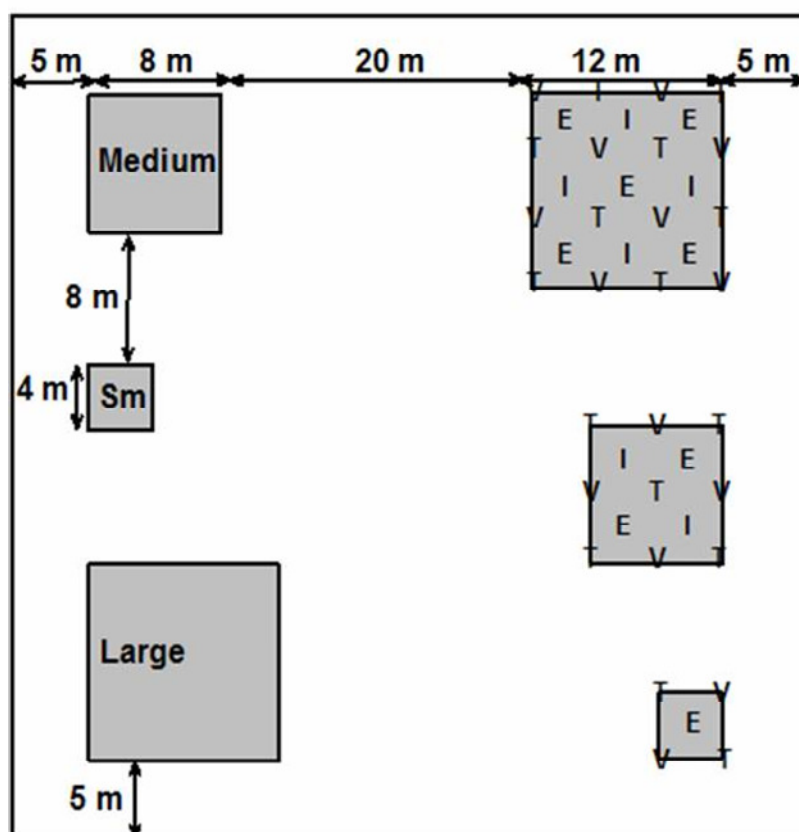
The study was conducted from 5 May-15 August 2007 and 11 May-8 August 2008 in restoration sites located near the town of Agua Buena (8° 44' N, 82° 58' W; elevation 1100-1300 m) in southern Costa Rica. Six restoration sites were planted in 2004 throughout a 30 km<sup>2</sup> area. The closest two sites were located 0.9 km apart and all other sites were at least 1.2 km apart. The next closest restoration site to each of the six sites ranged from 0.9-4.1 km away (mean  $\pm$  SD: 1.95  $\pm$  1.24 km). In the past 50 years most land surrounding Agua Buena was cleared for agricultural use, primarily for the production of sun coffee with some land used for pasture and subsistence agriculture. Currently, less than 27% of the original forest remains in the region, mostly in small fragments along waterways or on the mountains at higher elevations (Daily et al. 2001). The landscape surrounding the restoration sites is dominated by pasture, sparsely-shaded coffee and other agriculture, small human settlements and some patches of secondary and mature Pacific premontane humid forest (Daily et al. 2001; Sekercioglu

et al. 2007). All restoration sites had previously been used for  $\geq 18$  years for agriculture (usually coffee first and then pasture).

The restoration sites were planted with four seedling species: *Terminalia amazonia* (J.F. Gmel.) Exell [Combretaceae], *Vochysia guatemalensis* Donn. Sm. [Vochysiaceae], *Erythrina poeppigiana* (Walp.) O.F. Cook [Fabaceae], and *Inga edulis* Mart. [Fabaceae]. All species are native or naturalized to the region and are widely used in tropical forest restoration (Nichols et al. 2001; Carpenter et al. 2004). We conducted this study in all six sites in 2007, and in four of the six sites in 2008 due to logistical constraints. We used two experimental treatments at each site. Treatment plots were 50 x 50 m and either had (1) trees planted in rows to cover the entire plot (extra-large patch, 2500 m<sup>2</sup>), or (2) trees planted in six patches of three different sizes: two small (16 m<sup>2</sup>), two medium (64 m<sup>2</sup>) and two large patches (144 m<sup>2</sup>; Figure 1.1). Vegetation was cleared around planted trees every 2-3 months for the first two years of planting to allow seedlings to become established. The small number of seedlings that died during this time were replanted. No further clearing or planting was conducted after May 2006.

Tree heights ranged from 2-5 m in 2007. Extra-large patches had an almost continuous canopy over the 50 x 50 m treatment area. The large, medium and small patches remained distinct patches within a matrix of mostly herbaceous vegetation.

Figure 1.1: Planting arrangement at each restoration site. Each site had one 50 x 50 m extra-large patch (bottom) and one 50 x 50 treatment with six smaller patches (top): two large (12x12 m), two medium (8x8 m) and two small (4x4 m). Each side of the second treatment had one small, one medium and one large patch, although the arrangement of the patches varied among sites. The number and arrangement of the tree species within the patches was constant across all sites. Shaded areas are planted with trees. Tree species are indicated by letters: *Erythrina* (E), *Vochysia* (V), *Inga* (I), and *Terminalia* (T). Non shaded areas are non-woody vegetation, primarily grasses. Sm=small patch.



### *Patch Size Reclassification*

Although the number of seedlings planted in each plot was initially the same, seedling growth and mortality varied, resulting in variation in canopy cover among patch sizes and tree species. Thus we classified patch sizes based on canopy area, which sometimes differed from the original size classification. In both 2007 and 2008, we measured canopy cover for every tree in the small, medium and large patches and one-third of the trees (selected at random) in each extra-large patch. To measure individual tree canopy cover, we used the formula for the area of an ellipse ( $\pi d_1 d_2 / 4$ ); where  $d_1$ =the longest canopy diameter and  $d_2$ =the diameter perpendicular to  $d_1$ . This method of canopy cover approximation correlates with above-ground biomass (Peek 1970) and total leaf area (Kohyama and Hotta 1990) and has been used to describe forest structure in tropical secondary forests (Montgomery and Chazdon 2001). To calculate total canopy cover for each small, medium and large patch, we summed the canopy cover of all trees within each patch. For extra-large patches, we multiplied the average canopy cover of each tree species by the number of each species in that patch (Fink et al. 2009). We used the classification based on canopy cover in all further analyses.

There were several patches where birds were never observed. In 2007, no birds were observed in 15 of the 41 patches and in 2008, no birds were observed in 9 out of the 28 patches. The patches where no birds were observed were significantly smaller than those in which birds were observed (mean  $\pm$  SE, 2007: patches with birds:  $979.9 \pm 310.9 \text{ m}^2$ ; patches without birds:  $42.5 \pm 12.9 \text{ m}^2$ ;  $t_{39}=3.01$ ,  $P=0.006$ ; 2008: patches with birds:  $1251.1 \pm 473.2 \text{ m}^2$ ; patches without birds:  $62.1 \pm 25.8 \text{ m}^2$ ;  $t_{26}=3.12$ ,  $P=0.005$ ). Patches without bird observations were not included in further analyses.

Patches were reclassified based on canopy cover (see above). Patches that were initially planted as small ( $16 \text{ m}^2$ ), medium ( $64 \text{ m}^2$ ), and large ( $144 \text{ m}^2$ ) were reclassified to small (mean  $\pm$  SE, 2007:  $62.9 \pm 8.2 \text{ m}^2$ ,  $N=7$ ; 2008:  $78.3 \pm 5.5 \text{ m}^2$ ,  $N=4$ ), medium (2007:  $143.4 \pm 6.1 \text{ m}^2$ ,  $N=5$ ; 2008:  $134.0 \pm 10.6 \text{ m}^2$ ,  $N=3$ ), and large (2007:  $300.6 \pm 31.7 \text{ m}^2$ ,  $N=7$ ; 2008:  $342.0 \pm 39.7 \text{ m}^2$ ,  $N=8$ ) using total canopy cover. Since all extra-large patches had much greater total canopy cover (2007:  $3672.2 \pm 449.2 \text{ m}^2$ ,  $N=6$ ; 2008:  $5080.1 \pm 407.4 \text{ m}^2$ ,  $N=4$ ) than small, medium and large patches, their original classification of "extra-large" was retained. Reclassified patch sizes were used in all analyses.

### *Foraging Observations*

We conducted foraging observations of four species of insectivorous and omnivorous bird species in the restoration sites: Cherrie's tanager *Ramphocelus costaricensis*, rufous-capped warbler *Basileuterus rufifrons*, common tody-flycatcher *Todirostrum cinereum* and plain wren *Thryothorus modestus*. Cherrie's tanager is a frugivore-insectivore while the other species are primarily insectivores (Stiles and Skutch 1989). Cherrie's tanagers, rufous-capped warblers and plain wrens forage primarily by gleaning (picking food items from nearby substrates from a standing position, no acrobatic movements; Remson and Robinson 1982; Stiles and Skutch 1989). Common tody-flycatchers use both gleaning and sally-strike (flight directly at a prey item on substrate) manoeuvres, but rarely fly out to capture aerial insects (Stiles and Skutch 1989). These four species were the most commonly observed foliage-



gleaning insectivores in the restoration sites. There was no fruit available in the sites during the study, thus all observations were of birds foraging for arthropods.

In 2007, foraging observations were conducted from 5 May-15 August at five of the six restoration sites. Due to logistical constraints, foraging observations were conducted at the sixth site from 24 June-21 July 2007 only. In 2008, observations were conducted from 11 May-8 August at four of the six sites used in 2007. In both years, observations were conducted at each site approximately once every 10 days between sunrise and 1100 hours. Each site was systematically searched to locate foraging birds and observations were made on birds throughout each patch. Foraging observations lasted as long as the bird was in sight. For each observation, we recorded the bird species, number of prey attacks (attempts to capture insect prey), tree species where attacks occurred, and movements between attacks: hops, short flights (<1 m), and long flights (>1 m) (Pomara et al. 2003). Only those foraging bouts of at least 20 seconds were included for analysis (Robinson and Holmes 1982). All observations were continuously recorded on a digital voice recorder by E.B Morrison.

Time spent in non-foraging states (e.g. preening) was removed from the total observation time before calculation of attack rate, search effort, and vigilance (Lyons 2005). We calculated attack rate (number of attacks per minute) by dividing the total number of attacks by the total observation time (Pomara et al. 2003; Lyons 2005). Search effort (number of movements per attack) was calculated by dividing the total number of movements by the total number of attacks in each observation (Pomara et al. 2003). Vigilance was considered a measure of predation risk (Caraco et al. 1980; Glück

1987) and was recorded as the percentage of the observation a bird spent alert or scanning with bill horizontal or above (Repasky 1996; Bednekoff and Lima 2002).

Some birds were colorbanded which allowed individual identification. In 2007, ten Cherrie's tanagers, six rufous-capped warblers, two common tody-flycatchers, and two plain wrens were banded. In 2008, nine Cherrie's tanagers, seven rufous-capped warblers, three common tody-flycatchers and three plain wrens were banded. Rufous-capped warblers, plain wrens and common tody-flycatchers were paired and held territories during the study period (Stiles and Skutch 1989). Our observations of banded and paired individuals suggested that territory size was 1 ha or less for plain wrens, common tody-flycatchers and rufous-capped warblers. Jedlicka et al. (2006) reported a similar territory size for rufous-capped warblers. We identified two pairs of each of these three species at some sites, while other sites had only one pair.

Cherrie's tanagers are sexually dimorphic and found in loose groups of 4-10 individuals year-round (Stiles and Skutch 1989). Based on observations of banded individuals, the territories of Cherrie's tanager groups in our study included an entire restoration site (0.5 ha), with 6-10 individuals per site. In the same region a density of 12 Cherrie's tanagers per ha was reported by Krueger et al. (2008). The size of Cherrie's tanager group territories has not been reported in the literature. However extensive mist-netting in the restoration sites between 2006-2008 resulted in no recaptures of individuals between sites, although individuals are often recaptured within a site (Lindell, unpubl. data).

We estimated the number of individuals observed from sightings of paired and banded individuals and the locations of their territories within the restoration sites.

Additionally, we assumed that unbanded individuals at one site were different from unbanded individuals at another site because the sites were separated by distances much greater than the territory sizes of the bird species.

No more than one foraging observation was made per banded individual per day and we waited at least one day between recording observations of unbanded individuals of the same species (or sex for Cherrie's tanager) on the same site (Wagner 1981; Wunderle and Latta 1998; Johnson 2000; Pomara et al. 2003). We included multiple observations of the same individuals in our analysis because it ensured the inclusion of variability in the behavior of individual birds among patch sizes. Such observations were not truly independent, and their inclusion may have inflated sample sizes somewhat and led to an increased Type I error rate in statistical tests (Hurlbert 1984). However, the use of only a single observation of each individual would have weakened our ability to separate the effects of patch size on behavior from differences among individuals (Pomara et al. 2003). Thus we believe that the value of using multiple observations of single individuals outweighed the potential problems (e.g. Holmes, Bonney and Pacala 1979; Johnson 2000; Pelletier 2005; Lyons 2005; Jedlicka et al. 2006).

### *Arthropod Sampling*

General Methods - The four bird species we studied are primarily surface gleaners, taking insects directly from vegetation substrates such as leaves or branches (Stiles and Skutch 1989). Branch clipping was used to collect arthropod samples from branches and leaves (Johnson 2000). A collapsible bag was positioned around the outer 0.75-1.0 m of a selected branch, the mouth of the bag was closed, and the branch

clipped free with a tree pruner. Bags were visually inspected for arthropods and all arthropods were immediately categorized into 1 mm size intervals and identified to at least the Order level. The clipped vegetation was weighed to the nearest g using a Pesola scale (wet mass). We standardized the amount of arthropod biomass per vegetation biomass by dividing the wet mass of the arthropods in each sample by the wet mass of the clipped vegetation. Each sample is expressed as [(g of arthropod biomass/ g of clipped vegetation)\*1000]. This method is commonly used to measure food availability for birds (Johnson 2000; Johnson et al. 2005; Smith et al. 2006; Vitz and Rodewald 2006).

We identified arthropod species to the following categories: Aranae, Orthoptera, Dermaptera, Hemiptera, Homoptera, Coleoptera, Lepidoptera adults, Lepidoptera larvae, Diptera, Formicidae and other Hymenoptera (bees and wasps), unknown adults, and unknown larvae. Length-weight regressions from Johnson and Strong (2000) and Schoener (1980) were used to calculate arthropod biomass for all Orders. These Orders have been reported in the stomach samples of these species and analogous species in similar habitats (C.H. Sekercioglu pers. comm.; Poulin et al. 1994; Poulin and Lefebvre 1996).

*Weighted Insect Abundances* - Foraging observations and branch clip sampling were conducted concurrently. We selected the proportions of each of the four tree species for arthropod sampling based on estimations of tree species use by the four focal bird species, such that tree species with greater proportionate use formed a greater proportion of the invertebrate samples. Branch clip samples were taken from 17-30 trees in each extra-large patch, 5-8 trees in each large patch, 3-7 trees in each

medium patch, and 3-6 trees in each small patch. Numbers of trees sampled varied within patch sizes because of variation in tree mortality and growth rates. Trees used for arthropod sampling were located throughout each patch. Branch clip samples were taken from a range of heights that matched the range of prey attack heights for the four bird species in each year.

After the study period concluded, we found that the percentage of prey attacks was greater in *Inga* than in the other three tree species and the proportion of branch clippings among the four tree species did not match the percentage of prey attacks in each tree species. In both years we undersampled *Inga* and oversampled the other three tree species (Table 1.1).

Table 1.1: The percentage of prey attacks and percentage of arthropod samples in each tree species in 2007 and 2008.

Tree Species	2007		2008	
	% prey attacks	% arthropod samples	% prey attacks	% arthropod samples
<i>Terminalia</i>	1.8%	13.8%	1.6%	17.5%
<i>Vochysia</i>	6.6%	12.7%	2.9%	16.9%
<i>Erythrina</i>	4.5%	18.4%	10.4%	16.3%
<i>Inga</i>	87.1%	55.1%	85.1%	49.3%

To correct for this, we weighted branch clip samples from each tree species to match the proportions of prey attacks in each tree species. We used the following formula (adapted from Johnson 2000) for each tree species (*i*):

$$W_i = n_{\text{ideal}(i)} / n_{\text{actual}(i)} \quad \text{eqn 1}$$

$$n_{\text{ideal}(i)} = U_i * n_{\text{total}} \quad \text{eqn 2}$$

where

$W_i$  = the weighting factor by which all branch clip samples within tree species ( $i$ ) were multiplied,

$n_{ideal(i)}$  = the number of branch clip samples from tree species  $i$  if the match between proportions of attacks and branch clip sample distributions as precise,

$n_{actual(i)}$  = the actual number of branch clip samples taken from tree species  $i$ ,

$U_i$  = the per cent of attacks in tree species  $i$ ,

$n_{total}$  = the total number of branch clip samples from all tree species.

The weighted sample totals were used in calculations of arthropod abundance (Johnson 2000).

*Insect Sampling Period* - In 2007, five of the sites were sampled twice during the study; once between 21 May-10 June and once between 10-22 July. Branch clip samples at the sixth site were taken only once between 5-8 July because foraging observations were only conducted from 24 June-21 July. In 2008, every site was sampled twice; once between 5-8 June and once between 7-11 July. Arthropod abundance was calculated for each sampling period for each patch by summing the arthropod biomass from all branch samples taken in each patch and then dividing by the

sum of the branch weights for that particular patch. Arthropod abundance values for patches from the two sampling periods were strongly correlated (2007: Pearson's  $r=0.53$ ,  $P=0.01$ ; 2008:  $r=0.70$ ,  $P=0.001$ ). Therefore, within each year, arthropod samples from the two sampling periods were averaged, so that each patch had one arthropod abundance value.

### *Data Analysis*

Some patches changed size classes between years, i.e. they grew from medium in 2007 to large in 2008, so we analysed data from 2007 and 2008 separately in order to use data from the same patches in both years. All dependent variables (attack rate, search effort, arthropod abundance, vigilance) were checked for normality and homoscedasticity. Attack rate and search effort were log transformed to meet these assumptions. General linear models (GLM) were used to examine the effects of site, sex (Cherrie's tanager only) and patch size (small, medium, large and extra-large) on attack rates and search efforts for each of the four species. All factors except patch size were not significant ( $P>0.35$  for all factors) and removed from the models.

Vigilance data could not be normalized using transformation. Thus we used non-parametric Kruskal-Wallis ANOVAs to analyze the effects of patch size on per cent time spent vigilant. A GLM was used to examine the effect of site and patch size on arthropod abundance. The effect of site was not significant and was removed from the model. Tukey's *post hoc* analyses were used to examine pair-wise differences among the patch sizes for arthropod and foraging behavior data. All data were analysed using

SAS 9.1 (SAS Institute 2004). Throughout, we present results as mean  $\pm$  SE.

Differences between groups were considered significant when  $P < 0.05$ .

## RESULTS

### *Foraging Observations*

Total observation time across all sites was 237 hours in 2007 and 116 hours in 2008. Mean duration of foraging observations (mean  $\pm$  SE averaged across 2007 and 2008) was  $82.8 \pm 3.6$  sec for Cherrie's tanagers,  $85.8 \pm 4.8$  sec for rufous-capped warblers,  $65.4 \pm 5.4$  sec for common tody-flycatchers and  $80.4 \pm 7.2$  sec for plain wrens.

In 2007 (at six sites), we conducted 75 observations of at least 43 Cherrie's tanager individuals, 55 observations of at least 18 rufous-capped warblers, 22 observations of at least 14 common tody-flycatchers and 30 observations of at least 16 plain wrens. In 2008 (at four sites), we conducted 54 observations of at least 22 Cherrie's tanagers, 38 observations of at least 14 rufous-capped warblers, 28 observations of at least 12 common tody-flycatchers and 23 observations of at least 12 plain wrens.

### *Foraging Behavior*

In both 2007 and 2008, attack rate was significantly higher and search effort was significantly lower in larger patches than in smaller patches for Cherrie's tanagers, plain wrens and rufous-capped warblers (Figure 1.2; Table 1.2). Common tody-flycatchers



showed no differences among patch sizes for both search effort and attack rate in both years (Figure 1.2; Table 1.2).

Table 1.2: ANOVA results of the effect of patch size on attack rate and search effort for all four bird species in 2007 and 2008.

Species	2007			2008		
	<i>F</i>	d.f.	<i>P</i>	<i>F</i>	d.f.	<i>P</i>
Cherrie's tanager						
attack rate	5.6	3,71	<0.01	6.4	3,50	<0.01
search effort	7.0	3,71	<0.01	9.2	3,50	<0.01
Plain wren						
attack rate	4.0	2,27	0.03	5.5	3,19	<0.01
search effort	3.6	2,27	0.04	5.1	3,19	0.01
Common tody-flycatcher						
attack rate	2.1	3,18	0.14	0.3	2,25	0.74
search effort	0.9	3,18	0.44	0.8	2,25	0.50
Rufous-capped warbler						
attack rate	12.1	3,51	<0.01	7.1	2,35	<0.01
search effort	7.6	3,51	<0.01	4.4	2,35	0.02

Figure 1.2: Effect of patch size on attack rates in (a) 2007 and (b) 2008 and search effort in (c) 2007 and (d) 2008. E=extra-large patches, L=large patches, M=medium patches and S=small patches. Standard error bars are presented. Means with different letters are significantly different (Tukey,  $P<0.05$ ). CHTA=Cherrie's Tanager, PLWR=Plain Wren, CTFL=Common Tody-flycatcher, RCWA=Rufous-capped Warbler. There were no observations in the small patches of plain wrens in 2007 or common tody-flycatchers and rufous-capped warblers in 2008.

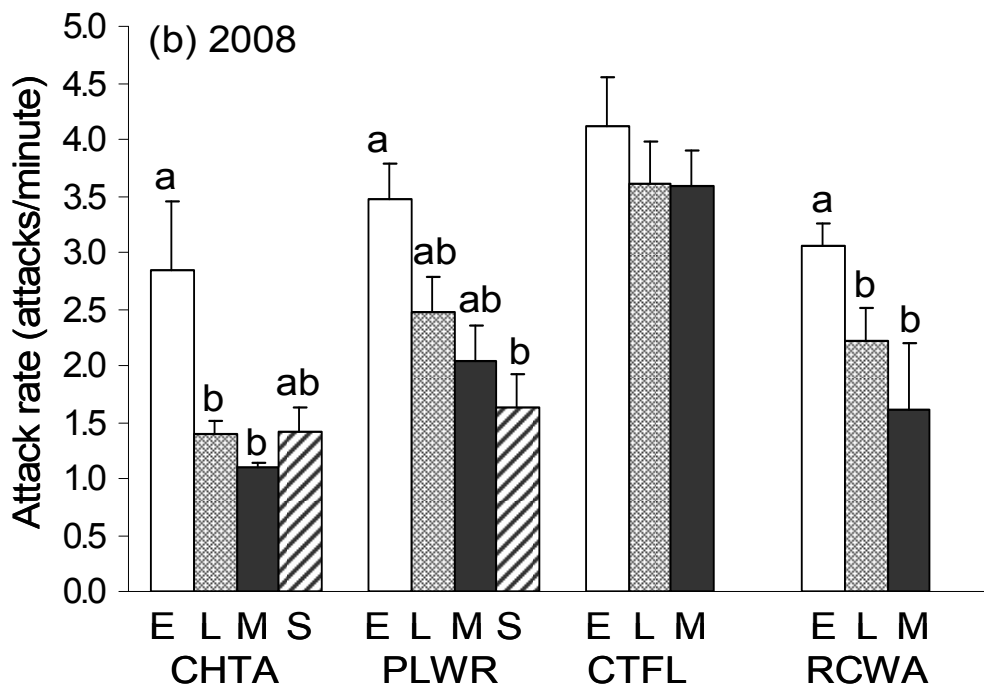
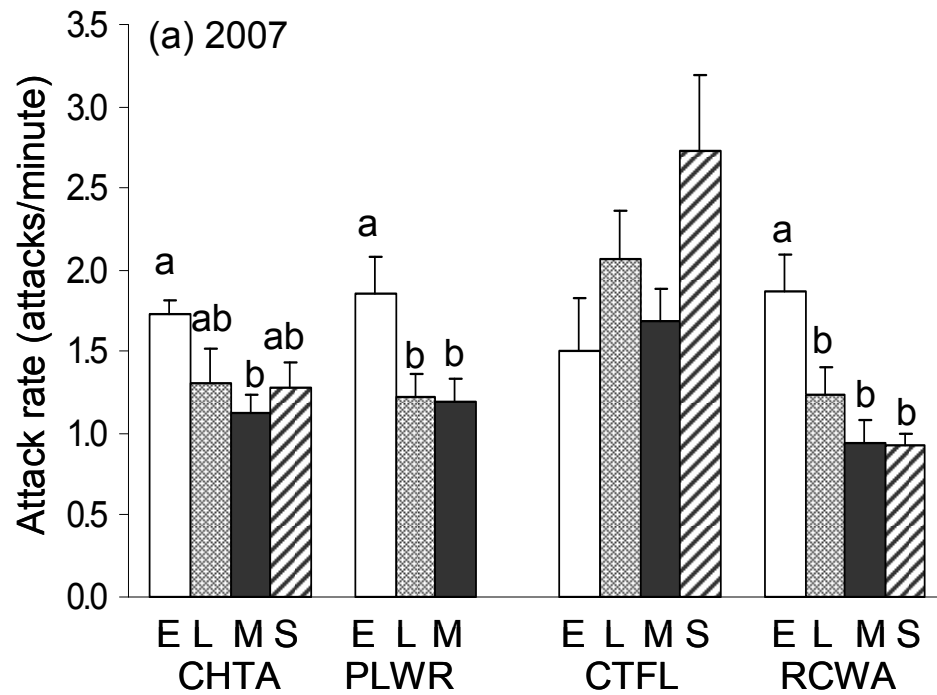
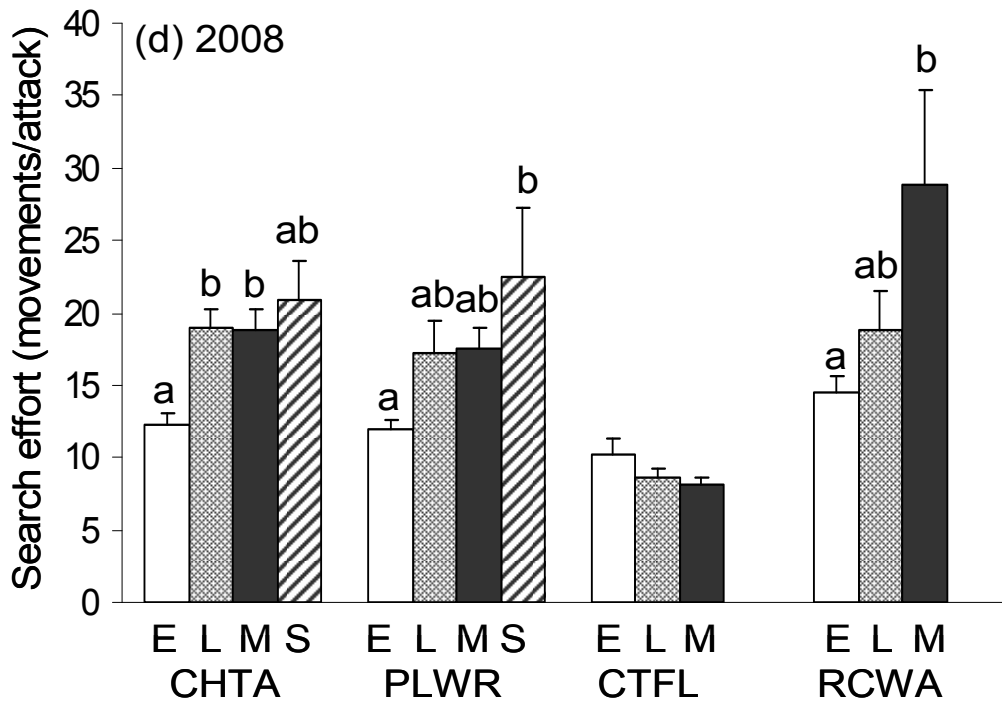
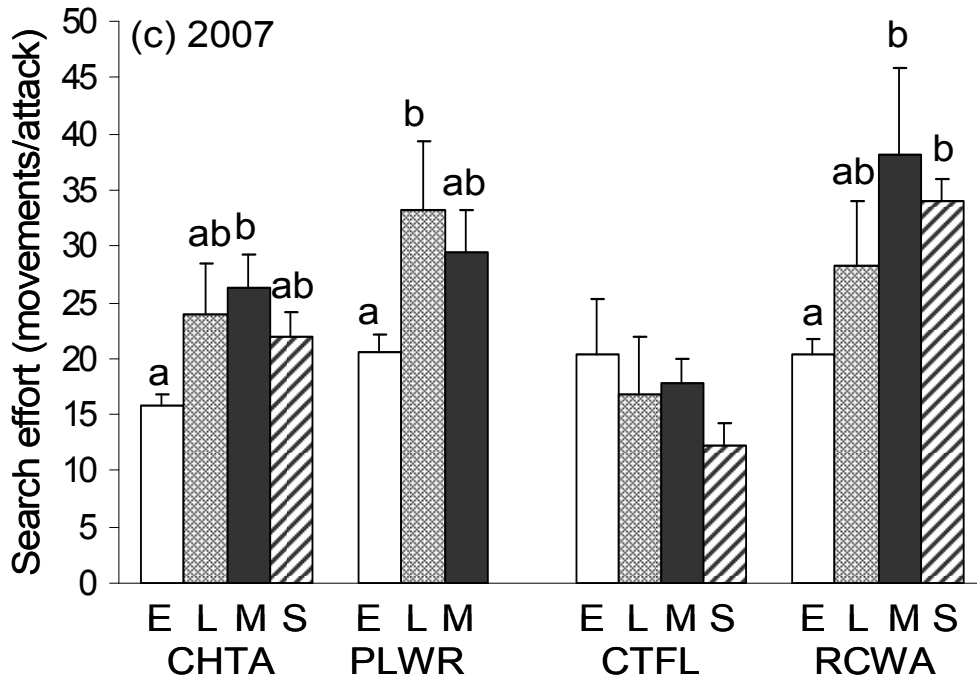


Figure 1.2 (cont'd)



### Arthropod Abundance

Patch size significantly influenced arthropod abundance in both years (Figure 1.3; 2007:  $F_{3,22}=14.5$ ,  $P<0.0001$ ; 2008:  $F_{3,15}=11.3$ ,  $P<0.0001$ ). In 2007, extra-large and large patches had higher arthropod abundance than either medium or small patches (Tukey,  $P<0.05$ ). In 2008, arthropod abundances in extra-large patches were greater than medium and small patches and arthropod abundances in large patches were greater than small patches (Tukey,  $P<0.05$ ).

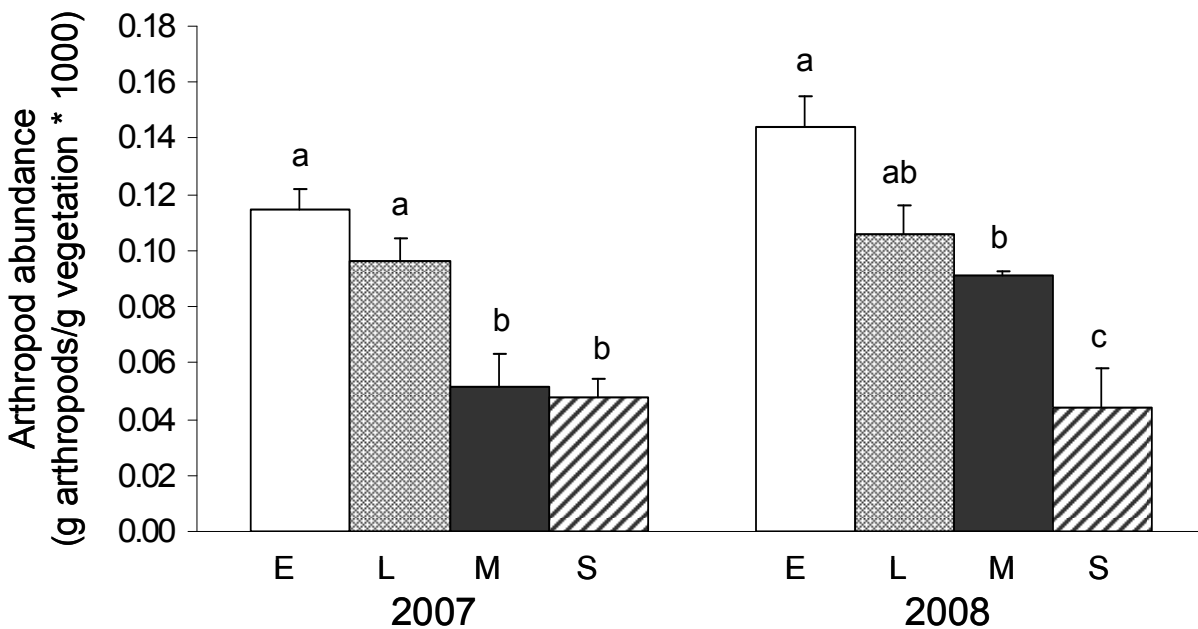
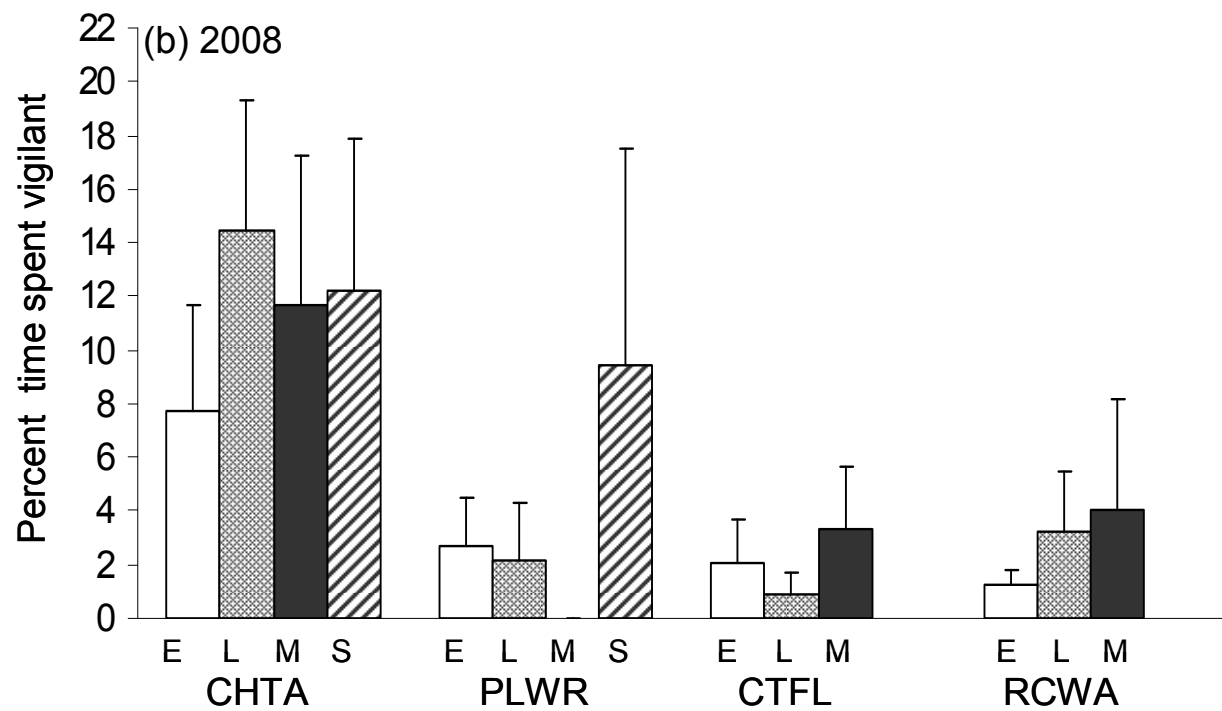
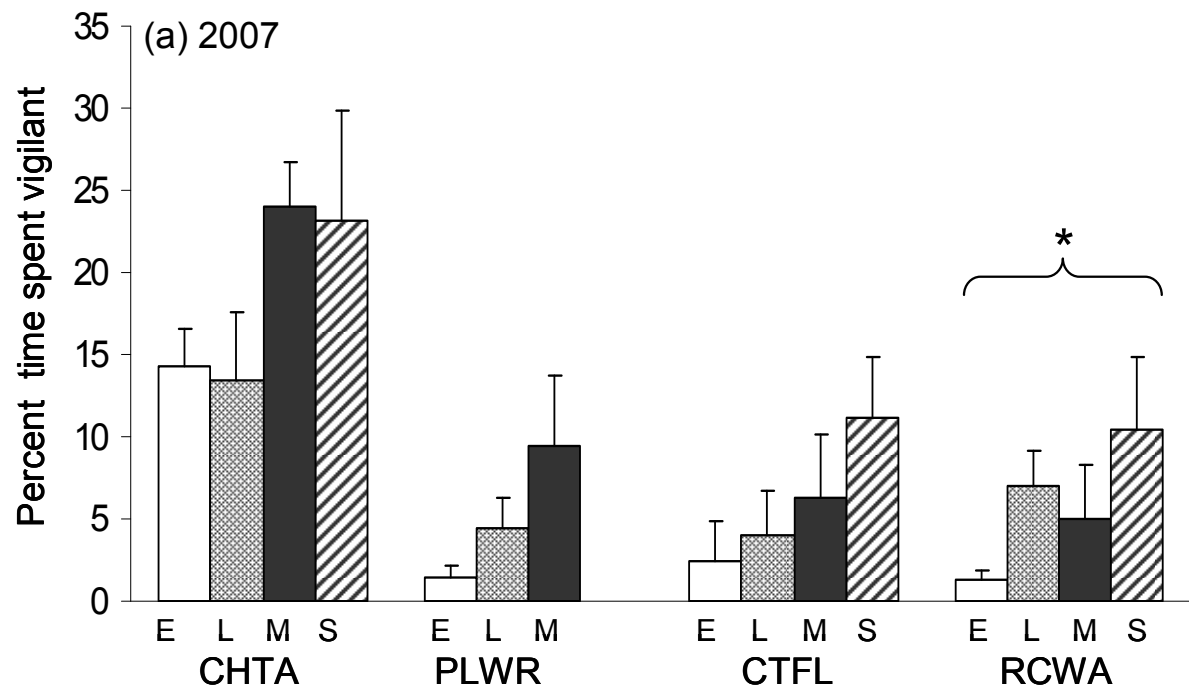


Figure 1.3: Effect of patch size on insect abundance [(g of arthropod biomass/ g of clipped vegetation)\*1000] in 2007 and 2008. E=extra-large patches, L=large patches, M=medium patches and S=small patches. Standard error bars are presented. Means with different letters are significantly different (Tukey,  $P<0.05$ ).

### Predation Risk

In 2007, vigilance was significantly higher in smaller patches for rufous-capped warblers (Figure 1.4a; Kruskal-Wallis ANOVA:  $H=18.8$ , d.f.=3,  $P=0.003$ ). Cherrie's tanagers had marginally higher vigilance in smaller patches (Figure 1.4a;  $H=6.6$ , d.f.=3,  $P=0.08$ ). Patch size did not affect vigilance for either plain wrens (Figure 1.4a;  $H=5.5$ , d.f.=2,  $P=0.11$ ) or common tody-flycatchers (Figure 1.4a;  $H=5.1$ , d.f.=3,  $P=0.16$ ). In 2008, there were no effects of patch size on vigilance for any of the four species (Figure 1.4b; Cherrie's tanagers:  $H=2.9$ , d.f.=3,  $P=0.40$ ; plain wrens:  $H=2.5$ , d.f.=3,  $P=0.48$ ; common tody-flycatchers:  $H=1.1$ , d.f.=2,  $P=0.57$ ; rufous-capped warblers:  $H=0.3$ , d.f.=2,  $P=0.85$ ).

Figure 1.4: Effect of patch size on predation risk (measured as vigilance) in (a) 2007 and (b) 2008. There were significant differences among patch sizes (indicated by asterisk) for only rufous-capped warblers in 2007. E=extra-large patches, L=large patches, M=medium patches and S=small patches. Standard error bars are presented. CHTA=Cherrie's Tanager, PLWR=Plain Wren, CTFL=Common Tody-flycatcher, RCWA=Rufous-capped Warbler. There were no observations in the small patches of plain wrens in 2007 or common tody-flycatchers and rufous-capped warblers in 2008. Vigilance was zero in the medium patches for plain wrens in 2008.





## DISCUSSION

Planting small patches of vegetation, of tens to hundreds of metres squared, is a potential alternative restoration strategy to planting over large areas (Rey Benayas et al. 2008). However this restoration strategy has not been widely implemented nor rigorously tested in comparison with other restoration methods. Using Web of Science, we systematically searched articles published in *Restoration Ecology*, *Ecological Applications* and the *Journal of Applied Ecology* from 1999-2009 to find studies that specifically examined patch size effects of planted woody vegetation on at least one restoration process. We also encountered papers from other journals on an ad-hoc basis. We found only four studies that considered patch size in analyses (Zahawi and Augspurger 2006; Fink et al. 2009; Munro et al. 2009; Selwood et al. 2009). Numerous studies, however, used replicated patches of planted seedlings equivalent in size to our small, medium and large patches to evaluate or compare restoration techniques such as irrigation and different soil preparation methods and their effects on phenomena such as seedling survival and growth (e.g. Burkett et al. 2005; Eränen and Kozlov 2006). The implicit assumption of these studies is that their results would be similar for planted patches of larger sizes. Given the results of this study and others, it is clear that patch size is an important variable to consider and that results from one patch size may not necessarily scale up or down to other patch sizes.

The effects of restoration patch size on the behavior of animals have received almost no attention (Fink et al. 2009) although animal activities such as foraging contribute to ecosystem recovery processes such as pollination, seed dispersal, and the regulation of herbivorous insect populations (Sekercioglu 2006). Our results showed

greater foraging success, i.e. higher prey attack rates and lower search effort, in larger patches (a few thousand metres squared) than in smaller patches (a few hundred metres squared or less) for three of the four species we studied. Patch size effects on foraging success are likely to have consequences for rates of energy acquisition and fitness (Lima and Dill 1990; Olsson et al. 2002). Thus, from the perspective of insectivorous birds, larger patches of planted trees provide more food for a given effort than smaller patches. We expect patch size effects for other insectivorous taxa, for example bats, would be similar. While planted patches of hundreds of metres squared may facilitate ecosystem recovery in some ways (Rey Benayas et al. 2008; Cole et al. 2010), our results indicate they will provide lower quality habitat than patches of several thousand metres squared for some animals whose presence and activities contribute to successful restoration. These differences may diminish over time as the patches spread and additional woody vegetation establishes naturally. Our results also demonstrate the value of using a behavioral ecological approach in the assessment of restoration patch quality. Behavioral observations, unlike species presence/absence data, provide information on the mechanisms likely to be driving patterns of patch use (Lindell 2008).

Previous studies on birds conducted in non-restoration contexts have used foraging behavior as a proxy measure of food availability to document a wide range of patterns, including variation in habitat characteristics (e.g. Pomara et al.; Lyons 2005). However, it is important to concurrently measure arthropod abundance to verify that foraging patterns reflect food availability. We found that arthropod abundance was higher in larger patches, indicating that our findings of higher prey attack rates and lower search effort in larger patches reflect variation in food availability among patch

sizes. Thus, attack rates and search effort are likely to be good indicators of food availability and habitat characteristics and a useful index of the value of a patch from the perspective of foraging animals (Johnson 2000; Pomara et al. 2003; Lewis et al. 2008).

We assumed that structural characteristics of smaller patches, including low canopy cover and high proportions of edge, would expose foraging individuals to greater predation risk from aerial predators than when they foraged in larger patches (Suhonen 1993; Kotler et al. 2004). Thus, we predicted that patch size would be a significant factor affecting vigilance, our measure of predation risk, but only rufous-capped warbler showed greater vigilance in smaller patches. Our data indicate that food availability is the primary driver of foraging differences across patch sizes while predation risk may be important only for some species in some years. However, methodological consideration may also have influenced the results on predation risk. When conducting observations, we assumed that foraging and vigilance were mutually exclusive and only measured overt scanning (head up with bill horizontal or above) as evidence of anti-predator vigilance (Fernández-Juricic et al. 2005). Recent studies show that some foraging birds use peripheral vigilance (while head is down foraging) in addition to overt scanning vigilance (Lima and Bednekoff 1999). The birds we studied may employ peripheral vigilance while foraging, which we were not able to measure. In addition, vigilance strategies may differ depending on the type of predators present. We assumed that predatory birds were the most important predators because we regularly observed them in the sites and the study species responded to them. Head-up vigilance is likely to be a good reflection of predation risk from predatory birds but may

be less representative of risk from mammals and reptiles, which we observed occasionally.

The objective of planting in small patches, i.e. tens to a few hundred metres squared, is to provide colonization foci in degraded lands where little native vegetation exists, using a fraction of the financial and labor resources required for planting seedlings to cover entire areas (Zahawi and Augspurger 2006). However, in choosing a restoration design it is important to balance economic benefits with ecological consequences and to prioritize the processes and species to be restored. We found that, in 3-4 year old restoration sites, larger patches ( $> 3500 \text{ m}^2$  of canopy cover) provide approximately twice the density of arthropods as smaller patches ( $< 350 \text{ m}^2$ ). This difference is reflected in the greater foraging success of insectivorous birds in larger patches. Tropical birds are key players in ecosystem functions (e.g. Van Bael et al. 2008) and forest birds are often a focus of conservation efforts because of tropical deforestation (Sodhi et al. 2008). Thus, forest restoration efforts using a patch-based planting scheme should consider patch size as an important factor that is likely to affect the quality of the patches as habitat for birds that use woody habitat. We recommend that small patches be avoided and that patches of at least a few thousand metres squared be planted when resources are available.

## CHAPTER 2

### ACTIVE OR PASSIVE FOREST RESTORATION? ASSESSING RESTORATION ALTERNATIVES WITH AVIAN FORAGING BEHAVIOR

#### INTRODUCTION

Conversion of forests to pastures for cattle grazing and other agriculture has created large areas of deforested and degraded land in the humid tropics (FAO 2005). Developing effective strategies to restore these lands is critical because of their high biodiversity and their significant role in processes such as water and carbon cycles (Brown 1993). Ecological restoration strategies can be divided into two broad categories. Passive restoration is where environmental stressors such as cattle grazing and agriculture are removed and colonization by shrubs and trees and secondary succession takes place naturally. Active restoration is where the land is managed by planting vegetation, weeding, burning and/or thinning to achieve a desired structure (Rey Benayas et al. 2008).

A limited number of studies have directly compared active and passive restoration and found that the regeneration pathways and resulting vegetation structure are likely to be significantly different (Parrotta 1992; Carnevale and Montagnini 2002; Florentine and Westbrooke 2004). Tropical restoration sites planted with tree seedlings had higher biomass (Parrotta 1992), understory tree density and diversity (Carnevale and Montagnini 2002) and greater seedling recruitment (Parrotta 1992; Florentine and Westbrooke 2004) than control sites that were not planted. However, Powers et al. (1997) found that seven-year old abandoned pastures were intermediate in understory vegetation species richness compared to monocultures of several different tree species.

Resulting differences in vegetation structure may influence several components of the habitat quality of passively versus actively restored sites for animals, including food availability. Canopy cover (Perfecto et al. 1997; Johnson 2000), structural heterogeneity (Basset et al. 2001; Richards and Windsor 2007) and plant species diversity (Holmes and Schultz 1988; Johnson 2000) are correlated with the biomass and distribution of arthropods. In turn, arthropod biomass influences the foraging patterns of animals that prey on arthropods, such as insectivorous birds (Maurer and Whitmore 1981; Robinson and Holmes 1982 Johnson 2000). Foraging attack rates (number of attacks on prey per unit time) have been shown to be positively associated with food availability for birds in both tropical (Johnson 2000; Morrison et al. 2010) and temperate habitats (Kilgo 2005; Lyons 2005). Attack rates, along with search effort (locomotor movements per attack), affect rates of energy acquisition and expenditure that can significantly affect fitness (Pomara et al. 2003; Butler et al. 2005; Lewis et al. 2008). Measuring these components of the habitat quality of restoration sites for birds is important because birds are significant contributors to ecological functions as pollinators (Feldman 2006), seed dispersers (Wunderle 1997) and consumers of herbivorous insects (Van Beal et al. 2003).

We evaluated vegetation structure and food availability (measured using both foraging behavior and arthropod biomass) between active and passive restoration treatments for three resident tropical bird species. Active and passive restoration sites in this study were part of a replicated forest restoration experiment in southern Costa Rica. Active restoration treatments were former pastures planted in 2004 with four species of tree seedlings in a uniform planting design. Passive restoration treatments were former

pastures burned once in 2003 and again in 2004, then abandoned to regenerate naturally over time.

We expected that the active treatment sites would have greater vegetation density in the highest canopy strata and greater heterogeneity in the vertical structure of the vegetation than the passive restoration treatments (Parrotta 1992; Carnevale and Montagnini 2002; Florentine and Westbrooke 2004). These vegetation characteristics have been shown to affect the biomass and distribution of arthropod prey, which in turn affect the foraging patterns of insectivorous birds (Holmes and Robinson 1981; Holmes and Schultz 1988, Johnson 2000). Thus we predicted that arthropod biomass and prey attack rates would be highest, and search efforts lowest, in the active restoration sites.

## METHODS

### *Study Sites*

The study was conducted from 15 May - 15 August 2008 in active and passive restoration sites in southern Costa Rica. The study sites were located between the Organization for Tropical Studies' Las Cruces Biological Reserve (hereafter Las Cruces; 8° 47' N, 82° 57' W) and the town of Agua Buena (8° 44' N, 82° 58' W; elevation 1100-1300 m). In the past 50 years, most land surrounding Agua Buena was cleared for agricultural use, primarily for the production of sun coffee with some land used for pasture and subsistence agriculture. Less than 27% of the original forest remains in the region, mostly in small fragments along waterways or in the mountains at higher elevations (Daily et al. 2001).

The active restoration sites ( $n = 4$ ) had previously been used for greater than 18 years for agriculture (typically coffee first and then pasture). Active sites were planted in 2004 with four species of tree seedlings: *Terminalia amazonia* (J.F. Gmel.) Exell [Combretaceae], *Vochysia guatemalensis* Donn. Sm. [Vochysiaceae], *Erythrina poeppigiana* (Walp.) O. F. Cook [Fabaceae], and *Inga edulis* Mart. [Fabaceae]. All species are native or naturalized to the region and are widely used in tropical forest restoration (Nichols et al. 2001; Carpenter et al. 2004). At each site a 50 x 50 m area was planted with trees in rows to cover the entire plot. Vegetation was cleared around planted trees every 2-3 months for the first two years after planting to allow seedlings to become established. The small number of seedlings that died during this time were replanted. No further clearing or planting was conducted after May 2006. Tree heights ranged from 2-10 m in 2008. Trees had formed an almost continuous canopy over each 50 x 50 m area.

The passive restoration sites ( $n = 2$ ) were located in the Melissa's Meadow (MM) section of Las Cruces. MM is a 31 ha tract of land that had been planted with *Pennisetum* grass species and used for cattle grazing until 1998, when Las Cruces acquired it. MM is located adjacent to the primary and secondary forest (250 ha) of Las Cruces. The passive sites were two 1 ha square plots (100 m apart) that were burned to clear the grass cover in February of 2003 and again in February of 2004 and subsequently abandoned. No vegetation was cleared prior to the burn treatments except for a 12 m fire break surrounding each 1 ha plot. After the burning, there was no vegetation standing, except for 2-3 remnant trees per plot that did not burn. Currently the sites are dominated by the native, woody species *Heliocarpus appendiculatus*



Turcz. [Tiliaceae], *Miconia trinervia* (Sw.) D. Don ex Loudon [Melastomataceae], *Cecropia* spp. (mostly *C. obtusifolia* and *C. peltata*) and several *Piper* spp.

One of the active restoration sites is also located within the MM section of Las Cruces, within 50 m of the mature forest of Las Cruces and between 100-300 m from the two passive sites. The other three active restoration sites are located 3-10 km away from Las Cruces. One of these three sites is located adjacent to a 43 ha mature forest. The other two sites were located in landscapes with small amounts of forest (10-20% secondary forest within a 500 m radius surrounding the site, Cole et al. in press). All four active restoration sites were at least 3 km apart from each other.

### *Foraging Observations*

We conducted foraging observations of three species of insectivorous and omnivorous birds in the restoration sites: Cherrie's Tanager (*Ramphocelus costaricensis*), Rufous-capped Warbler (*Basileuterus rufifrons*) and Common Tody-flycatcher (*Todirostrum cinereum*). Cherrie's Tanager is a frugivore-insectivore while the other species are primarily insectivores (Stiles and Skutch 1989). These three species were the most commonly observed foliage-gleaning insectivores in the restoration sites. All observations were of birds foraging for arthropods rather than fruit.

Observations were conducted from 11 May - 8 August 2008 and were conducted at each site approximately once every 7-10 days between sunrise and 1100 hours. Each site was systematically searched to locate foraging birds and observations were made on birds throughout each site. Foraging observations lasted as long as the bird was in sight. For each observation, we recorded the bird species, number of prey

attacks (attempts to capture insect prey), and movements between attacks: hops, short flights (<1 m), and long flights (>1 m) (Pomara et al. 2003). Only foraging bouts of at least 20 seconds were included in analyses (Robinson and Holmes 1982). All observations were continuously recorded on a digital voice recorder by E.B Morrison.

We defined 'total observation time' as the number of minutes during which a focal bird was watched, minus the number of minutes in which it was engaged in activities other than foraging (i.e. preening; Lyons 2005). We calculated attack rate (number of attacks per minute) by dividing the total number of attacks by the total observation time (Pomara et al. 2003; Lyons 2005). Search effort (number of movements per attack) was calculated by dividing the total number of movements by the total number of attacks in each observation (Pomara et al. 2003).

Some birds were color-banded which allowed individual identification. A total of ten Cherrie's Tanagers, nine Rufous-capped Warblers and five Common Tody-flycatchers were colorbanded across all sites used in this study. Based on sightings of color-banded individuals and birds in pairs, we estimated that two pairs of Rufous-capped Warblers and Common Tody-flycatchers were using each of the active restoration sites. Each passive restoration sites had at least two pairs of each of these species. Cherrie's Tanagers are sexually dimorphic and found in loose groups year-round (Stiles and Skutch 1989). Based on observations of banded individuals, the Cherrie's Tanager groups in our study were 6-10 individuals in size, which matched reported group sizes in the same region (Krueger et al. 2008). The one active and two passive restoration sites located within the MM section of Las Cruces may have been close enough that the same Cherrie's Tanagers used all three sites. The other three

active sites were located far enough apart from each other and from MM (3-10 km) that the individuals at these sites were different.

No more than one foraging observation was made per banded individual per day and we waited at least one day between recording observations of unbanded individuals of the same species (or sex for Cherrie's tanager; Wunderle and Latta 1998; Johnson 2000; Pomara et al. 2003). We included multiple observations of the same individuals in our analysis because it ensured the inclusion of variability in the behavior of individual birds (e.g. Johnson 2000; Lyons 2005; Jedlicka et al. 2006). Such observations were not truly independent, and their inclusion may have inflated sample sizes somewhat and led to an increased Type I error rate in statistical tests (Hurlbert 1984).

### *Arthropod Sampling*

General Methods - The focal bird species are primarily surface gleaners, taking insects directly from vegetation substrates such as leaves or branches (Stiles and Skutch 1989). A method called branch clipping was used to collect arthropod samples from branches and leaves (Johnson 2000). A collapsible bag was positioned around the outer 0.75-1.0 m of a selected branch, the mouth of the bag was closed and the branch clipped free with a tree pruner. Bags were visually inspected for arthropods and the clipped vegetation weighed to the nearest g using a Pesola scale. All arthropods were immediately categorized into 1 mm size intervals and identified at least to the level of order. To standardize for variable amounts of clipped vegetation, each sample is expressed as  $[(\text{g of arthropod biomass} / \text{g of clipped vegetation}) * 1000]$ .

Every site was sampled for arthropods twice; once between 4-8 June and once between 7-11 July 2008. We identified species to the following categories: Aranae, Orthoptera, Dermaptera, suborder Heteroptera (order Hemiptera), suborder Homoptera (order Hemiptera), Coleoptera, Lepidoptera adults, Lepidoptera larvae, Diptera, Formicidae (ants) and other Hymenoptera (bees and wasps), unknown adults, and unknown larvae. Length-weight regressions from Johnson and Strong (2000) and Schoener (1980) were used to calculate arthropod biomass for all insect categories. These insect groups have been reported in the stomach samples of the focal bird species and analogous species in similar habitats (C.H. Sekercioglu 2009, personal communication; Sekercioglu et al. 2002; Poulin et al. 1994; Poulin and Lefebvre 1996).

Foraging observations and branch clip sampling were conducted concurrently. As a result, we selected the proportions of tree species for arthropod sampling based on approximations of tree species use by the three focal bird species (measured as proportion of attacks that occurred in each tree species). Branch clip samples were taken from 25-30 trees in each active site and 60 trees in each passive restoration site. In the passive restoration sites, trees used for sampling included mostly *H. appendiculatus*, *M. trinervia*, *Cecropia* spp. and *Piper* spp. These tree species were the most common species in the sites and the most commonly used by foraging birds. Trees used for arthropod sampling were located throughout each site. Branch clip samples were taken from heights that matched the range of prey attack heights for the three bird species

**Weighted Branch Samples** - After the field work concluded, we found that in the actively restored sites, the percentage of prey attacks was greater in *Inga* than in the

other three tree species for each of the bird species. The proportion of branch clippings among the four tree species did not match the percent of prey attacks in each tree species (see Morrison et al. 2010). We undersampled *Inga* and oversampled the other three tree species. Measures of food availability should take into account the bird's foraging activity, use of certain tree species or locations within the habitat (e.g., Hutto 1990; Poulin and Lefebvre 1997). Thus, we weighted branch clip samples from each tree species to match the proportions of prey attacks in each tree species (see Morrison et al. 2010 for details of the weighting procedure).

The weighted sample totals were used in calculations of arthropod biomass for active sites (Johnson 2000). The proportions of branch clip samples in trees in the passive sites approximately matched the proportions of prey attacks in those tree species. Thus we did not correct the arthropod samples from the passive restoration sites.

### *Vegetation Sampling*

We characterized the vegetation structure of each treatment by measuring tree size (diameter at breast height, dbh), tree species diversity, tree density and vertical foliage profiles to measure the percent vegetation cover at different subcanopy strata at each site. Circular sampling plots of 16 m diameter (0.02 ha) were established in each of the four active sites (two plots in each site) and in the two passive sites (three plots in each). The location of the vegetation sampling plots were chosen at random. In each plot, vegetation was sampled at 21 points located at 1.6 m intervals along the north, south, east and west radii of the plot (Wunderle and Waide 1993). A 3 m tall pole

marked at 0.5 m intervals was placed vertically at each sample point. We recorded the presence or absence of foliage touching the pole within each height class. For height intervals above 3 m, we sighted along the pole (the observer stood at the base of the pole) and recorded the presence/absence of foliage in each of the following estimated height intervals: 3-4, 4-6, 6-8, 8-10, 10-12 and 12-15 m. For each height interval, percent vegetation cover was calculated by dividing the number of points in which foliage was present in that height interval by the total number of sample points ( $n = 21$  per plot) and multiplying by 100.

We also measured the dbh of each tree greater than or equal to 3 cm in diameter within the circular plot and calculated an average dbh for each sampling plot. We counted the number of trees ( $\geq 3$  cm dbh only) in each circular plot and used those data to calculate average tree density per hectare. We estimated tree species richness by counting the number of different tree species in each circular plot and averaging over the multiple plots per site.

### *Data Analysis*

We used Principle Components Analysis (PCA) to determine which vegetation characteristics explained most of the variance among restoration treatments. We condensed the 12 height intervals into four categories: 0-1.5 m (understory), 1.5-3 m (midstory), 3-8 m (subcanopy) and  $>8$  m (canopy) (Pejchar et al. 2005). These four height intervals were included in the PCA along with average dbh and tree density per site. Before performing the PCA analyses, we standardized the variables to account for differences in variable units (Gotelli and Ellison 2004).

All dependent variables were checked for normality and homoscedasticity. Attack rate and search effort were log transformed to meet these assumptions. We used t-tests to examine the effect of restoration treatment (active or passive) on average tree dbh and density in the vegetation sampling plots. We used t-tests to examine the effect of restoration treatment on attack rate and search effort for the three bird species, using the values from individual observations as the dependent variable. We also ran t-tests using the mean foraging behavioral values per plot (four active and two passive treatment plots) as the dependent variable, to compare average foraging behavior between the active and passive treatments. This latter test was done to assess the potential influence of having multiple observations from some individual birds in some of the plots. We used general linear models (GLM) to examine the effect of restoration treatment, the time of day at which arthropod samples were collected and sampling period (June and July) on arthropod biomass (measured as g of arthropod biomass/ g of clipped vegetation)\*1000) . All data were analyzed using SYSTAT (SAS Institute 2004). Throughout, we present results as mean  $\pm$  SE and differences between groups were considered significant when  $p < 0.05$ .

## RESULTS

### *Vegetation*

The two restoration treatments showed substantial differences in vegetation structure (Figure 2.1). The first two principle components combined explained 75.2% of the variance. The first principle component explained 46.9% of the variance and separated the vegetation sampling plots in the two restoration treatments based on

average tree dbh and percent vegetation cover in the understory vs. overstory. Passive treatments had smaller tree dbh and greater percent vegetation cover in the understory and midstory, while the active treatments had greater tree dbh and a much sparser understory and midstory. The second principle component explained 28.3% of the variance and separated the vegetation sampling plots in the treatments based on tree density. The active treatments consistently had low density while the passive sites showed substantial variability in tree density.

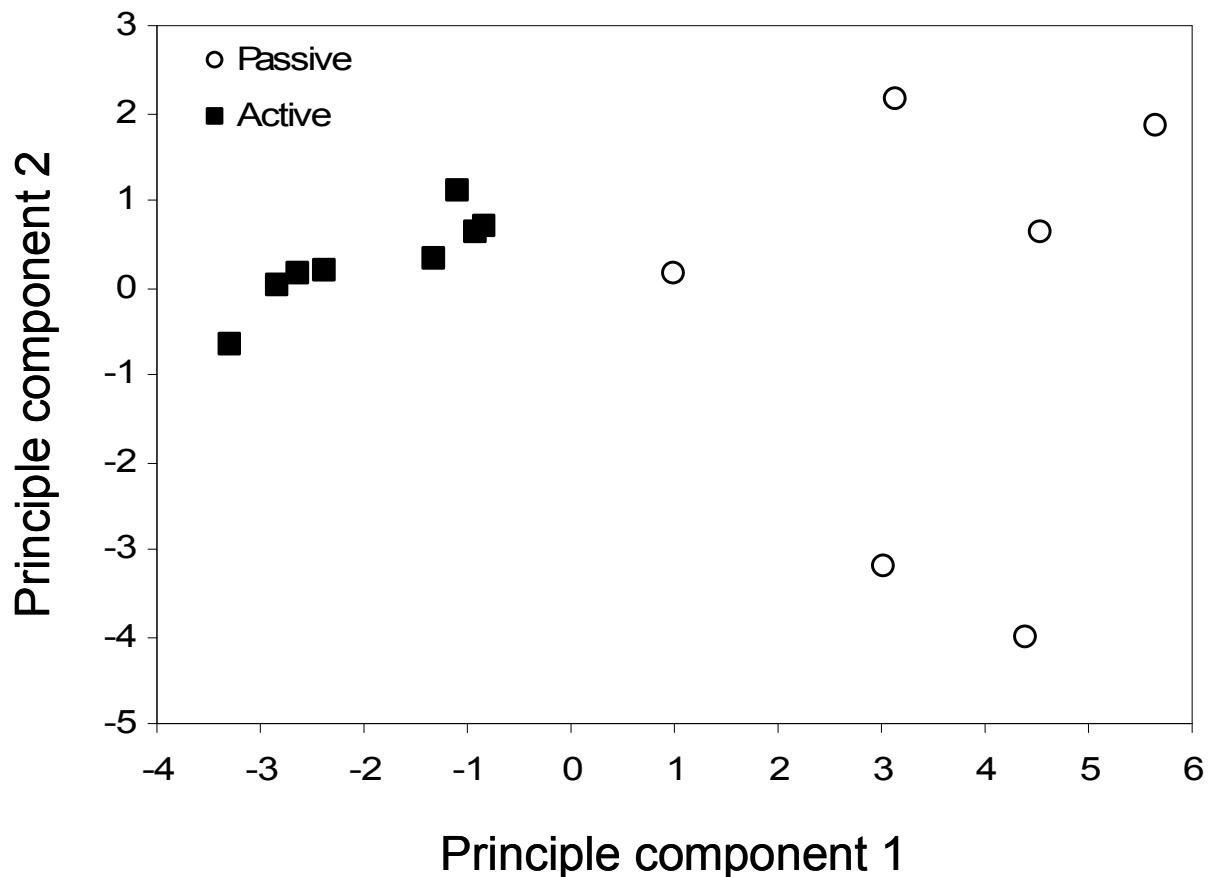


Figure 2.1: Principle components 1 and 2 from the PCA of habitat variables in the two restoration treatments (Active = 8 sampling plots, Passive = 6 sampling plots). Treatments are represented by symbols.



The active treatments had only four species of trees, while the number of tree species in the passive treatments ranged from 7-12. The vertical foliage height profiles confirmed results from the PCA and showed that the active treatments had much sparser understory and midstory while the passive treatments had greater understory and midstory cover (Figure 2.2). While both treatments had almost complete canopy cover, active treatments had a fairly uniform canopy height of 6-8 m tall while passive treatments had less uniform canopy height (Figure 2.2). Average dbh of trees in the active restoration treatments was significantly larger than in the passive treatments ( $t = -5.15$ ,  $df = 12$ ,  $p < 0.001$ ). Tree density was significantly higher in the passive treatments ( $t = 3.21$ ,  $df = 12$ ,  $p = 0.007$ ).

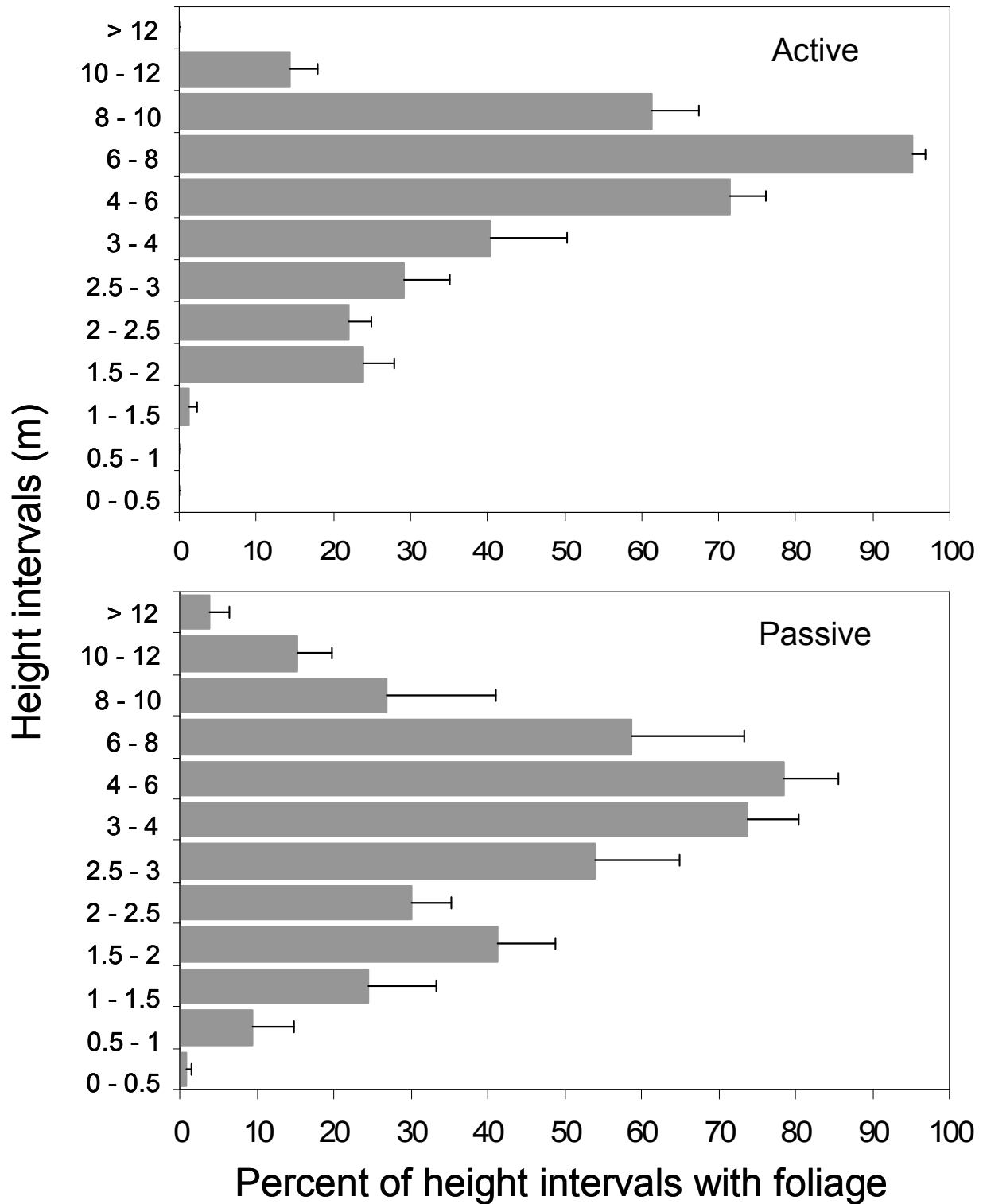


Figure 2.2: Foliage height profiles of the active and passive restoration treatments. These values were averaged across the multiple sampling plots per site and used to produce vertical foliage height profiles. Standard error bars are presented.

### *Arthropod Biomass*

There was no difference in arthropod biomass between active and passive restoration sites ( $F_{1,453} = 1.98$ ,  $p = 0.23$ ). There was no effect of time of day ( $F_{1,453} = 0.037$ ,  $p = 0.20$ ) or sampling period (June or July) on arthropod biomass ( $F_{1,453} = 2.32$ ,  $p = 0.18$ ).

### *Foraging Behavior*

Total observation time across all sites was 169 hours. Mean duration of foraging observations (mean  $\pm$  SE) was  $0.98 \pm 0.05$  min for Cherrie's Tanagers ( $n = 43$ ),  $1.07 \pm 0.06$  min for Rufous-capped Warblers ( $n = 45$ ) and  $0.89 \pm 0.07$  min for Common Tody-flycatchers ( $n = 22$ ).

Cherrie's Tanager showed no difference in either attack rate ( $t = -1.79$ ,  $df = 41$ ,  $p = 0.08$ ) or search effort ( $t = 1.80$ ,  $df = 41$ ,  $p = 0.08$ ) between the active and passive restoration treatments. Results were similar for Rufous-capped Warbler (attack rate:  $t = -0.20$ ,  $df = 43$ ,  $p = 0.84$ ; search effort:  $t = -1.84$ ,  $df = 43$ ,  $p = 0.07$ ) and Common Tody-flycatcher (attack rate:  $t = 0.45$ ,  $df = 20$ ,  $p = 0.66$ ; search effort:  $t = -0.47$ ,  $df = 20$ ,  $p = 0.65$ ).

Mean foraging behavioral values showed no significant differences for all three species for either attack rate (Cherrie's Tanager:  $t = 0.85$ ,  $df = 4$ ,  $p = 0.45$ ; Rufous-capped Warbler:  $t = 0.40$ ,  $df = 4$ ,  $p = 0.71$ ; Common Tody-flycatcher:  $t = 0.01$ ,  $df = 4$ ,  $p = 0.94$ ) or search effort (Cherrie's Tanager:  $t = 1.35$ ,  $df = 4$ ,  $p = 0.25$ ; Rufous-capped Warbler:  $t = 0.64$ ,  $df = 4$ ,  $p = 0.56$ ; Common Tody-flycatcher:  $t = 0.12$ ,  $df = 4$ ,  $p = 0.91$ ).

These results suggest that multiple observations from individual birds within treatments did not skew foraging behavior patterns.

## DISCUSSION

Food availability is an important component of habitat quality that is influenced by vegetation structure (Holmes and Robinson 1981; Johnson 2000; Johnson 2007). In our study area, passive restoration treatments had greater tree species diversity, denser and smaller trees, and a greater percent vegetation cover in the understory than did the active treatments. Despite these differences, arthropod biomass was not different between the active and passive treatments and avian foraging behavioral measures reflected these patterns of food availability. All three bird species showed no significant differences in prey attack rate and search effort between the two restoration treatments, indicating rates of energy acquisition are likely similar between the treatments.

Numerous studies have found that attack rates are greater and search effort lower when arthropod availability is higher. For example, Hooded Warblers (*Wilsonia citrina*) had lower attack rates near hardwood forest gaps than in the interiors, which corresponded with lower arthropod abundance (Kilgo 2005). Johnson (2000) found that attack rates of several Neotropical migrant species closely matched the patterns of arthropod biomass among shade coffee farms, citrus plantations and dry forests in Jamaica. American Redstart (*Setophaga ruticilla*) attack rates and arthropod densities were highest on temperate lake shorelines when compared to inland areas (Smith et al. 2007). Our previous work in the study sites showed that attack rates were higher and search efforts lower in restoration patches with the highest arthropod biomass (Morrison

et al. 2010). Thus, arthropod biomass and bird attack rates are consistently positively related.

The availability of food in a habitat affects an organism's energy intake and expenditure, which ultimately affects fitness (Pomara et al. 2003; Butler et al. 2005; Lewis et al. 2008). Our data on foraging behavior and arthropod biomass suggest that active and passive sites are approximately equal in food availability for insectivorous birds. However, other important components of habitat quality for insectivorous birds, including nest site availability, predation risk and reproductive success (Johnson 2007) were not measured in this study and could have differed between active and passive restoration sites.

The active and passive restoration sites had similar land-use histories and time since abandonment. Therefore, these potential influences on vegetation trajectories were controlled. The restoration sites located within the MM section of Las Cruces (one active and the two passive sites) showed strikingly different structure, suggesting that restoration strategy (passive or active) was the primary influence on vegetation structure. This is in accord with previous work that shows that tree species diversity, density and vegetation structure in planted sites are significantly different when compared to passive sites (Cusak and Montagnini 2004; Florentine and Westbrooke 2004). Passive sites tend to be influenced most by the characteristics of the local vegetation surrounding the sites (Günter et al. 2007), while the vegetation structure and tree species found on active restoration sites depends strongly on the characteristics (pioneer vs. mature-phase) and diversity of the tree species planted (Carnevale and

Montagnini 2004; Firn et al. 2007), the planting density (Vesk et al. 2008) and the type of maintenance done on the sites after planting (Piotto et al. 2003).

One potential influence on vegetation structure and, potentially, on arthropod biomass and foraging behavior, that we were not able to address was the effect of landscape. The active restoration sites were located in landscapes that varied in forest cover within a surrounding 500 m radius. The seedlings planted in all the active sites grew well and each of the sites developed a closed canopy. In addition, the patterns of arthropod biomass and foraging behavior of birds in the active sites were consistent over a range of landscapes (high to low forest), suggesting that landscape was not a significant influence on vegetation, arthropods, or birds in the active sites. In contrast, both passive sites were located adjacent to mature forest. Previous studies have shown that distance to forest is an important influence on forest regeneration in degraded lands, in part because of the greater availability of seeds in sites close to forest (Holl 1999). Thus, it is possible that passive sites in our study region located in less forested landscapes would have had less tree diversity and smaller trees, which could influence arthropod biomass and avian foraging behavior. Future work should compare the effectiveness of active versus passive restoration strategies in a paired design in landscapes with a range of forest cover.

The decision to use active or passive strategies in restoration projects should be based on the restoration project goals, budget, and site and landscape characteristics. Given that the recovery of passive restoration sites will depend strongly on land use history, time since abandonment and, potentially, landscape factors (Chazdon 2003), lands that have been used intensively, are severely degraded, and that are far from

seed sources may not recover naturally and could benefit from a more active restoration strategy (Wijdeven and Kuzee 2000; Günter et al. 2007). Our results suggest that passive restoration in high-forest cover landscapes in our study region is equally as effective as active restoration, from the perspective of insectivorous birds.

The costs of the two restoration strategies are substantially different (Chazdon 2008). Passive restoration requires no management costs except to eliminate the factors that caused the original degradation (i.e. grazing, agriculture). The passive sites in this study were burned twice to remove grass cover and were then left to regenerate. Each burning event took place over one day, required labor only to clear a fire break around each plot, and set and monitor the burn. No further labor or monitoring were needed after the final burn (R. Quiros 2009, personal communication). Active restoration is generally more costly and labor intensive than passive restoration (Rey Benayas et al. 2008). For the active restoration treatments in this study, costs included the purchase of tree seedlings, labor costs to clear sites and plant seedlings, the purchase and application of fertilizers and post-planting site maintenance (including clearing around seedlings). Including planting and labor, costs were \$120-180 per 100 tree seedlings planted, or approximately \$900-1400 per hectare (for two years of site maintenance; Zahawi and Holl 2009). Given the differences in costs, and the similar effectiveness of the two strategies, passive restoration would be preferred in high-forest cover landscapes in the study region.

## CHAPTER 3

### VIGILANCE BEHAVIOR OF A TROPICAL BIRD IN RESPONSE TO INDIRECT AND DIRECT CUES OF PREDATION RISK

#### INTRODUCTION

Animals must balance the costs and benefits of foraging in particular habitat patches (Brown 1988; Kilpatrick 2003). Costs such as predation risk can have significant effects on an individual's foraging decisions (Lima and Dill 1990; Nystrand 2007). Animals use a number of behavioral strategies to enhance the probability of predator detection, for instance, by increasing vigilance (Barnard 1980; Lima 1992; Lima and Bednekoff 1999; Whittingham et al. 2004), foraging in less risky habitats, or reducing travel distances to food sources (Cresswell 1999).

Vigilance is a common anti-predator defense mechanism to reduce predation risk in the short-term. However, vigilance often reduces food intake and foraging efficiency (Elgar 1989) and over the long-term, increased vigilance could potentially have a negative impact on fitness through a higher risk of starvation (Watson et al. 2007) or lack of adequate energetic resources to allocate to reproduction (Wolff and Van Horn 2003; but see Lind and Cresswell 2005).

Animals likely use multiple environmental cues to assess predation risk (Lima and Dill 1990). Indirect cues of predation risk are not provided by the predator itself, but are correlated with the likelihood of detecting, encountering and succumbing to a predator (Thorson et al. 1998). For example, habitat structure, such as canopy cover or habitat patch size, might be an indirect cue of an individual's risk of detection by a predator or the probability of escape from a predator (Thorson et al. 1998; Orrock et al. 2004).



Indirect cues such as the physical characteristics of a habitat may provide relatively consistent information about predation risk from a variety of potential predation threats (Blumstein et al. 2000; Orrock et al. 2004). However, indirect cues only allow animals to assess their potential, but not actual, predation risk at any given moment and they tend to overestimate risk when predators are absent and underestimate risk when predators are present (Sih 1992; Orrock et al. 2004).

In contrast, direct cues, particularly auditory and visual cues of a predator, are highly reliable. However, by the time potential prey detect a predator by a direct cue, they may not be able to respond successfully. Thus animals likely integrate both indirect and direct cues to evaluate their risk of predation. Studies in rodents show that animals respond more strongly to live or model predators when foraging in risky environments (open or illuminated habitats) than in safe environments (covered or dark habitats) (Kotler et al. 1991; Schmidt 2006). Other rodent studies have shown that foragers perceive a greater predation risk in response to indirect cues, such as degree of habitat cover or illumination, than to direct cues, such as predator scent, when both are present (Thorson et al. 1998; Orrock et al. 2004).

Birds are also likely to use multiple cues to assess predation risk. Much evidence shows that birds increase vigilance in response to both indirect cues, such as visual obstructions (Elgar 1989; Whittingham et al. 2004) and amount or type of vegetation cover (Eckman 1987; Carrascal and Alonso 2006), and direct cues of predator presence, including vocalizations (Hauser and Caffrey 1994) and model predators (Sullivan 1994). However no study has combined both types of cues to empirically

examine whether birds rely more on direct or indirect cues, or a combination of both types.

I examined the effects of indirect and direct cues of predation risk on the vigilance behavior of a tropical omnivorous bird, Cherrie's Tanager (*Ramphocelus costaricensis*), in a controlled field experiment. Habitat patches of different sizes were planted with four species of trees in 2005 as part of a large-scale experimental tropical forest restoration study. Restoring woody habitat by planting small patches of vegetation, of tens to hundreds of square meters, is an increasingly common type of forest restoration strategy (Rey Benayas et al. 2008). It is important that forest restoration efforts using a patch-based planting scheme consider patch size as an important factor that is likely to affect the quality of the patches as habitat for birds (Morrison et al. 2010). The habitat structure of these types of restoration are likely to influence behaviors, such as vigilance, that are could have potential negative fitness effects (Alcock 2005).

I used feeders placed at three different locations, the center and edge of a large patch and at the center of a small patch, as indirect cues of predation risk from an aerial predator. We assumed that small patches, and the edges of large patches, represented riskier habitat for foraging birds than the center of large patches because the structural characteristics of these locations, including low amount of canopy cover and high proportions of edge, would expose foraging individuals to greater predation risk than if they foraged in the center of large patches (e.g. Suhonen 1993; Kotler et al. 2004; Carrascal and Alonso 2006). Vocalization playbacks of a common falcon predator and non-predator bird (control) were used as direct cues of predation risk. I then recorded

the vigilance response of birds to the two playback treatments in each of the three feeder locations.

I tested the hypothesis that indirect cues of predation risk would influence several different measures of vigilance behavior, including time spent alert, head-turn frequency, the frequency and duration of head-up bouts, and latency to flee the feeder, in response to a direct cue of predation risk. If birds are using both types of cues to assess predation risk, then the change in vigilance response from pre- to post-playback of the predator vocalization will be highest in small patches and at the edges of large patches and lowest in large patches.

## METHODS

### *Research Sites*

The study was conducted from June to July 2008 in restoration sites located near the town of Agua Buena (8° 44' N, 82° 58' W; elevation 1100-1300 m) in southern Costa Rica. Four restoration sites were planted in 2005 throughout a 30 km<sup>2</sup> area. The closest two sites were located 3 km apart and all other sites were at least 5 km apart. In the past 50 years most land surrounding Agua Buena was cleared for agricultural use, primarily for the production of sun coffee with some land used for pasture and subsistence agriculture. Currently, less than 27% of the original forest remains in the region, mostly in small fragments along waterways or on the mountains at higher elevations (Daily et al. 2001). The landscape surrounding the restoration sites is dominated by pasture, sparsely-shaded coffee and other agriculture, small human settlements and some patches of secondary and mature Pacific premontane humid

forest (Daily et al. 2001; Sekercioglu et al. 2007). All restoration sites had previously been used for more than 18 years for agriculture.

The restoration sites were planted with four seedling species: *Terminalia amazonia* (J.F. Gmel.) Exell [Combretaceae], *Vochysia guatemalensis* Donn. Sm. [Vochysiaceae], *Erythrina poeppigiana* (Walp.) O.F. Cook [Fabaceae], and *Inga edulis* Mart. [Fabaceae]. All species are native or naturalized to the region and are widely used in tropical forest restoration (Nichols et al. 2001; Carpenter et al 2004).

I used two experimental treatments at each site. Treatment plots were 50 x 50 m and either had (1) trees planted in rows to cover the entire plot (plantation, 2500 m<sup>2</sup>), or (2) trees planted in six patches of three different sizes: two small (16 m<sup>2</sup>), two medium (64 m<sup>2</sup>) and two large patches (144 m<sup>2</sup>). Vegetation was cleared around planted trees every 2-3 months for the first two years of planting to allow seedlings to become established. The small number of seedlings that died during this time were replanted. No further clearing or planting was conducted after January 2007.

Tree heights ranged from 3-9 m in 2008. Plantation plots had an almost continuous canopy over the 50 x 50 m treatment area. The large, medium and small patches within the island plots remained distinct patches within a matrix of herbaceous vegetation.

### *Study Species*

Cherrie's Tanagers are sexually dimorphic and found in loose groups of 4-10 individuals year-round (Stiles and Skutch 1989). Based on observations of banded individuals, the territories of Cherrie's Tanager groups in our study included an entire

restoration site (0.5 ha), with approximately 6-10 individuals per site. In the same region a density of 12 Cherrie's Tanagers per ha was reported by Krueger et al. (2008). The size of Cherrie's Tanager group territories has not been reported in the literature. However extensive mist-netting in the restoration sites between 2006-2008 resulted in no recaptures of individuals between sites, although individuals are often recaptured within a site (Lindell, unpubl. data). Individuals in this study were colorbanded for identification.

### *Experimental Design*

Feeders baited with bananas were placed at three locations within each of the four restoration sites: center of the plantation (hereafter Large Center), within 4m of the edge of the plantation (hereafter Large Edge) and within 4m of the edge of one large island (hereafter Small; selected at random from the two large islands in the island treatment). Thus  $N=4$  for each of the three feeder location treatments. Large Edge feeders were located along an edge of the plantation that bordered fields consisting of mostly non-woody vegetation with few to no trees present. Small feeders were placed 4m from the edge of the island. The feeders were small wooden platforms (approximately 10x25 cm) placed on a stand 1.5m tall with three nails hammered into the surface of the platform to secure bananas. Feeders were set up in all sites in mid-May and left in place for the duration of the experiment. Feeders were baited with bananas for several days immediately after set-up to attract birds.

There were two experimental periods of four days each: 15-18 June and 5-8 July 2008. On Day 1 of each experimental period, the experiment was conducted at Site 1,

on Day 2, Site 2 was used, etc. Feeders were baited with bananas one day before each experimental trial. On the day of each trial, fresh bananas were placed on the feeders at 5:00am.

I simulated high predation risk using calls of a Barred Forest-falcon (*Micrastur rufficollis*), a common raptor in the landscape that preys on birds (Thorstrom 2000; Panasci and Whitacre 2002). The low predation risk treatment used calls of a Plain Wren (*Thryothorus modestus*), a common insectivore found in the restoration sites that has a loud song and is unlikely to be a food or territorial competitor with Cherrie's Tanager (Stiles and Skutch 1989; E.B Morrison pers. obs). One ten second recording was made for the Barred Forest-falcon and one for the Plain Wren. Each recording comprised two different songs for Plain Wren and two different call types for the Barred Forest-falcon. Songs for both species were taken from Ross (1998) and had been recorded in Puntarenas, Costa Rica. Hereafter I refer to the high predation risk playback as the Falcon treatment and the low predation risk (or control) treatment as the Wren treatment.

On each day, feeder locations (Small, Large Center, Large Edge) were randomly chosen for each of three two-hour time blocks. Between 5:30-7:30am, playbacks were conducted at one feeder location, the second feeder location between 7:30-9:30am and the third feeder location between 9:30-11:30am. Feeder locations were rotated among time blocks for both experimental periods so that each location was used in each time block at least twice (across all sites).

At each feeder location, I randomly chose a playback order (Falcon then Wren, or vice versa). When a bird landed and began feeding at the feeder, I started recording

using a digital video camera. After 25 seconds, either the Falcon or Wren call was played (10 s duration) and I continued recording until the bird left the feeder. I then waited at least 20 minutes, and repeated the playback procedure on a different individual using the other playback type. No more than two individuals were tested per feeder location per time block. Thus on one day, three Falcon calls and three Wren calls were played at each site. The experiment was only conducted on birds that were alone on the feeder platform. No individual was used more than once in this experiment.

The observer and video camera (JVC Everio Digital Camcorder GZ-MG360) were set up at least 20m from the feeder and hidden behind vegetation. The playbacks were broadcast at a standard sound level using a small speaker (LG MSP-100 Portable Stereo Speaker) placed 5 m from the feeder and connected via a cable to an MP3 player (Sansa Clip 1GB MP3 Player) controlled by the observer.

### *Behavioral Observations*

Windows Movie Maker 2.1 was used to analyze videos frame by frame at 0.1 second intervals. I measured behavioral variables for a 50-s observation period (Martin and Bateson 1986; Adams et al. 2006) that was divided into two 25-s periods; a 25-s pre-playback period, immediately followed by a 25-s observation post-playback period that included the 10-s playback of the vocalizations.

I measured five types of vigilance behavior for both the pre-playback and post-playback periods. First, the proportion of time a bird spends alert, with head-up and bill horizontal, is positively correlated with a response to increased predation risk in birds and other animals (Elgar 1989). I also measured the frequency of head-up bouts

(number of times bird raised its head from below horizontal to horizontal and above) and average duration of each head-up bout, which should increase with increased predation risk to facilitate quick detection of predators (Whittingham et al. 2004). The frequency of 'head-turns', scored as a lateral turn of at least 90 degrees of the focal bird's head, while vigilant in an upright posture with bill at least horizontal, can increase the quantity and the quality of information gathered by allowing individuals to scan a wider portion of space (Jones et al. 2007). I also measured the latency to flee the feeder as the time from the playback onset until the bird left the feeding platform. Latency to flee may reflect the level of fear birds have of the predation threat (Ramakrishnan and Coss 2000; Adams et al. 2006).

Some birds left the feeder before the 25-s post-playback period had elapsed. Thus I measured both pre- and post-playback behavioral variables as a proportion of the pre- and post-playback observation times. Fourteen of 36 individuals left the feeder before the 25-s post-playback period ended (mean  $\pm$  SE of post-playback duration for birds that left early,  $12.06 \pm 2.50$  s). Birds from six of the 14 observations (all six from the Falcon call treatment) left within 5-s ( $2.38 \pm 0.63$  s) of the initiation of the playback. I felt that this was not sufficient time to record meaningful data for most of the behavioral measures. For these six observations I recorded the proportion of time spent alert as 1.0 (100%) and did not record data for the other variables (i.e. frequency of head turns, head-up bouts, etc.). Sample sizes for each of the dependent measures of vigilance behavior are reported in Table 3.1.



Table 3.1: Sample sizes by treatment for the dependent measures of vigilance behavior. Total number of individuals tested was 36. For most birds, measurements for all five vigilance behaviors were collected. For those individuals that left the feeder less than five seconds after playback initiation, only time spent alert and latency to flee were measured. 'All others' includes head turn frequency, average duration of head-up bouts and frequency of head-up bouts.

Treatments	Dependent measures of vigilance behavior	
	Time spent alert and latency to flee	All others
Small		
Falcon	7	4
Wren	5	5
Large Center		
Falcon	5	5
Wren	7	7
Large Edge		
Falcon	6	3
Wren	6	6

### *Data Analysis*

I used repeated measures general linear models (GLM) to examine the effects of the indirect cue of feeder location (Large Center, Large Edge and Small) and the direct cue of playback treatment (Falcon, Wren) on the change in vigilance behavioral measures from pre-playback to post-playback. The vigilance behaviors (dependent variables) examined were (1) proportion of time spent alert, (2) head turn frequency (measured as the number of lateral head turns per minute), (3) frequency of head-up bouts (measured as the number of head-ups per minute) and (4) the average duration (in seconds) of each head-up bout. The change in behavior from pre- to post-playback was the within-subject factor. I included experimental period (June or July), site (one of four sites), time block (5:30-7:30, 7:30-9:30 or 9:30-11:30 am), sex (M or F) and the

interaction between feeder location and playback treatment as between-subject factors in the models.

I used ANOVA to examine the effects of feeder location and playback treatment on latency to flee (number of seconds the bird stayed at the feeder after initiation of the playback). I included experimental period, site, time block and sex in the models as independent variables. I used interaction contrasts to do pairwise comparisons of the effects of playback treatment on the vigilance behavior variables both within and across the three feeder locations.

All data were analysed using SPSS 18 for Windows (SPSS, Inc. 2009). Throughout, I present results as mean  $\pm$  SE. Differences between groups were considered significant when  $P < 0.05$ . All variables were checked for normality. Latency to flee was log transformed. All repeated measures GLM models met the sphericity assumption.

## RESULTS

### *Proportion of time spent alert*

Both feeder location ( $F_{1,23}=3.70$ ,  $P=0.04$ ) and playback treatment ( $F_{1,23}=31.4$ ,  $P<0.001$ ) significantly affected the change in proportion of time spent alert from pre- to post-playback. All other factors in the model were not significant (all  $F\leq 0.98$ , all  $P\geq 0.42$ ).

When comparing within feeder location, the proportion of time spent alert increased significantly after the Falcon playback compared to after the Wren playback in all three feeder locations (Small:  $P<0.01$ ; Large Edge:  $P<0.01$ ; Large Center:  $P=0.03$ ; Figure 3.2a). For birds exposed to the Falcon treatment, pairwise comparisons across feeder locations showed that the change in the proportion of time spent alert was significantly greater in both the Small and the Large Edge locations when compared to Large Center locations ( $P\leq 0.01$  for both; Figure 3.2a). However, difference between the Small and Large Edge locations were not significant ( $P=0.67$ ; Figure 3.2a). For birds exposed to the Wren playback, the change in proportion of time spent alert did not vary significantly among feeder locations (all pairwise comparisons  $P\geq 0.48$ ; Figure 3.2a).

### *Frequency of head turns*

Playback treatment significantly affected the change in head turn frequency from pre- to post-playback ( $F_{1,17}=4.80$ ,  $P=0.04$ ). However, feeder location did not affect the change in the frequency of head turns ( $F_{2,17}=2.49$ ,  $P=0.11$ ). All other factors were not significant (all  $F\leq 2.04$ , all  $P\geq 0.16$ ).

When comparing within feeder location, head turn frequency increased significantly after the Falcon playback compared to after the Wren playback for birds at

feeders in the Small locations ( $P=0.02$ ), but not in the Large Edge ( $P=0.65$ ) or Large Center locations ( $P=0.23$ ; Figure 2b). For birds exposed to the Falcon treatment, pairwise comparisons across feeder locations showed that the change in the frequency of head turns was greater in Small locations than in Large Center locations, but this difference was not significant ( $P=0.06$ , Figure 3.2b). There were no significant differences between the Small and Large Edge locations ( $P=0.90$ ) or between the Large Edge and Large Center locations ( $P=0.10$ ; Figure 3.2b). Head-turn frequency did not vary significantly among the three feeder locations for birds exposed to the Wren playback (all pairwise comparisons  $P \geq 0.43$ ; Figure 3.2b).

#### *Average duration of head-up bouts*

Playback treatment significantly affected the change in average duration of head-up bouts from pre- to post-playback ( $F_{1,17}=8.40$ ,  $P=0.01$ ). Feeder location did not affect the average duration of head-up bouts ( $F_{2,17}=0.97$ ,  $P=0.40$ ). All other factors were not significant (all  $F \leq 2.58$ , all  $P \geq 0.13$ ).

There was a significant increase in the average duration of head-up bouts after the Falcon playback than after the Wren playback within the Small feeder locations ( $P=0.01$ ; Figure 3.1c). Birds in the Large Center and Large Edge locations also showed a greater increase in average duration of head-up bouts after the Falcon playback than after the Wren playback, but these differences were not significant (Large Center,  $P=0.06$ ; Large Edge,  $P=0.07$ ; Figure 3.1c). For birds exposed to the Falcon treatment, pairwise comparisons across feeder locations showed that the change in the frequency of head turns was greater in Small locations compared to Large Center locations, but

this difference was not significant ( $P=0.07$ , Figure 3.1c). There were no significant differences between the Small and Large Edge locations ( $P=0.15$ ) or the Large Edge and Large Center locations ( $P=0.86$ ; Figure 3.1c). Head-up bouts did not differ across the three feeder locations for birds exposed to the Wren playback (all pairwise comparisons  $P\geq 0.88$ ; Figure 3.1c).

Figure 3.1: Mean change in (a) proportion of time spent alert, (b) frequency of head-turn bouts (measured as head-turns per minute) and (c) average duration of head-up bouts (measured in seconds) from pre- to post-playback for birds exposed to the Falcon and Wren treatments at each feeder location (Small Patch, Large Patch Edge, Large Patch Center). Asterisks represent significant differences ( $P < 0.05$ ) between the Falcon and Wren playback treatments within feeder location. Letters represent pairwise comparisons among the Falcon treatments across locations (different letters represent significant differences at  $P < 0.05$ ). If no letters are present, there were no significant differences across locations.

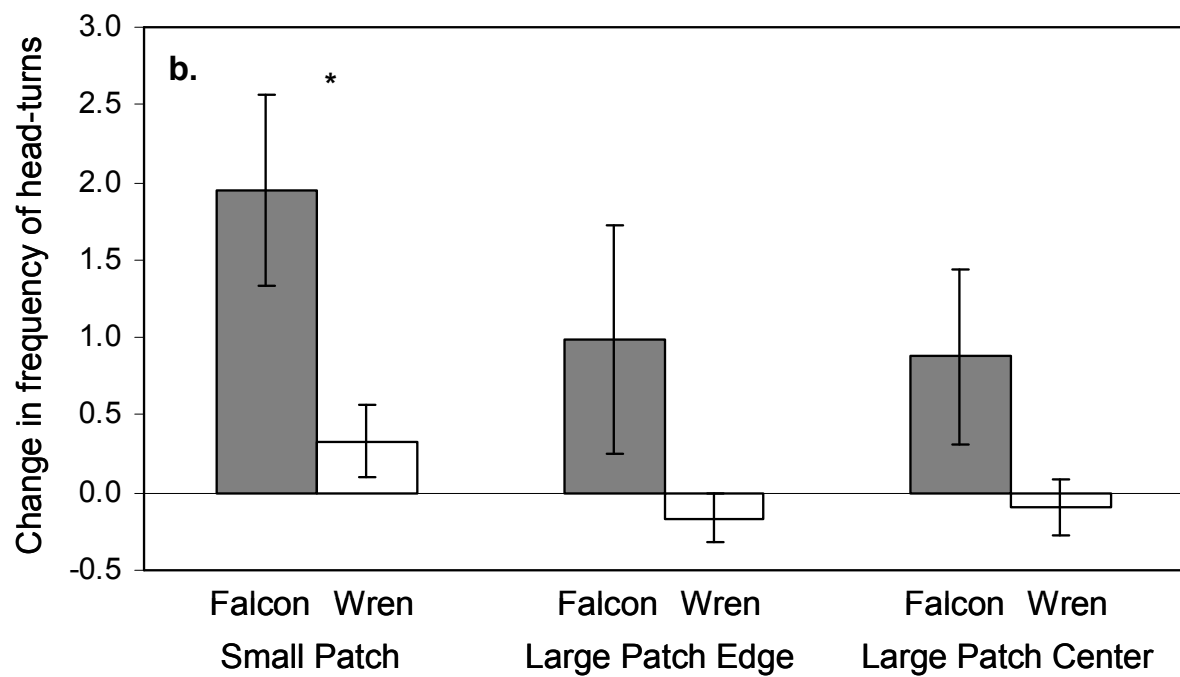
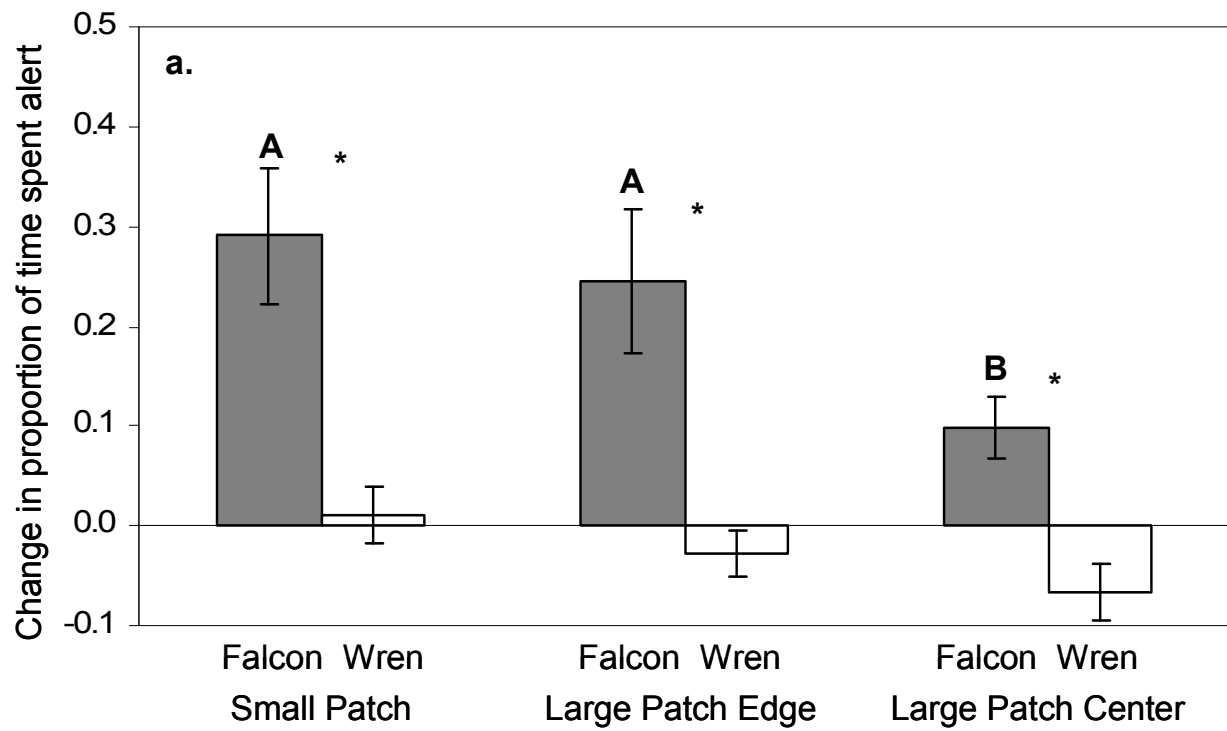
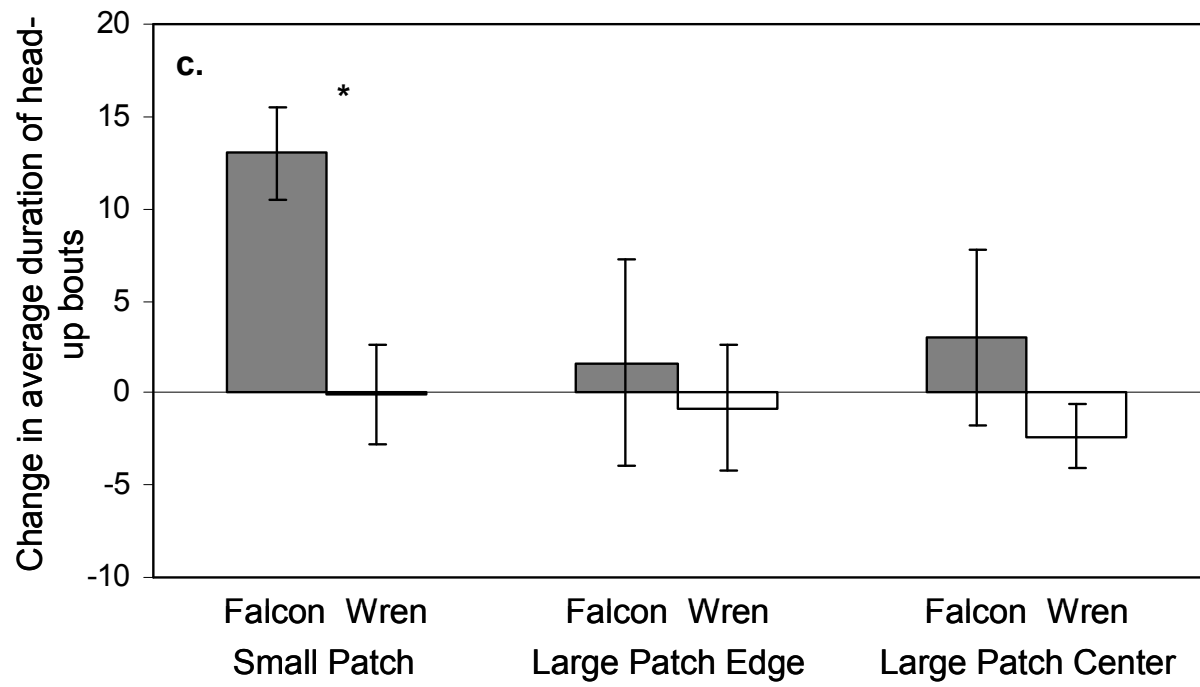


Figure 3.1 (cont'd)





### *Frequency of head-up bouts*

Neither playback treatment ( $F_{1,16}=0.83$ ,  $P=0.37$ ) nor feeder location ( $F_{2,16}=0.76$ ,  $P=0.48$ ) had a significant effect on the change in frequency of head-ups (measured as the number of head-ups per minute) from pre- to post-playback) and no other factors had a significant effect on the model (all  $F \leq 1.66$  and  $P \geq 0.22$ ).

### *Latency to flee*

Birds left the feeder significantly faster after the Falcon treatment than after the Wren treatment (mean  $\pm$  SE across all feeder locations: Falcon =  $27.5 \pm 8.8$  s; Wren =  $50.9 \pm 16.6$  s;  $F_{1,24}=4.53$ ,  $P=0.04$ ). However, there was no effect of feeder location on latency to flee ( $F_{2,24}=2.25$ ,  $P=0.13$ ). All other model terms were not significant (all  $F \leq 0.74$ , all  $P \geq 0.49$ ; Figure 3.2).

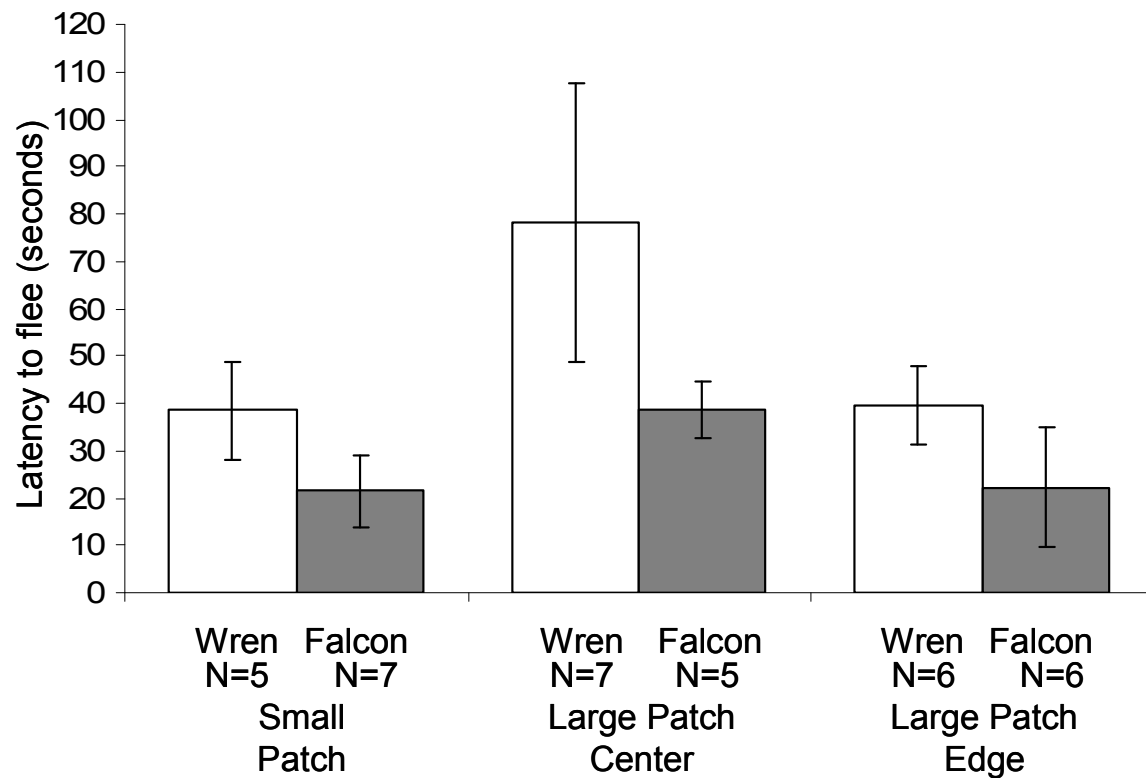


Figure 3.2: Mean latency to flee (measured as the number of seconds the bird stayed at the feeder after initiation of the playback; log transformed) for birds exposed to the Falcon and Wren treatments at each feeder location (Small Patch, Large Patch Center, Large Patch Edge).

## DISCUSSION

Both direct and indirect cues of predation risk influenced the vigilance behavior of foraging Cherrie's Tanagers. Birds in all three feeder locations increased time spent alert in response to the predator call compared to the non-predator call, similar to other studies that show birds increase vigilance in response to direct cues of predation risk including vocalizations (Hauser and Caffrey 1994) and model predators (Sullivan 1994). However, the indirect cues of patch size and location within the patch mediated the alert response to the direct cue of predator vocalizations. The change in time spent alert in

response to the predator call was significantly greater in the presumably riskier small patches and the edges of large patches compared to the relatively safe center of large patches. These results match studies in rodents showing that animals respond more strongly to live predators or predator vocalizations when foraging in risky environments, such as open or illuminated habitats, than safe environments, including covered or dark habitats (Kotler et al. 1991; Schmidt 2006). The structural characteristics of smaller patches, including low amount of canopy cover and high proportions of edge, would expose foraging individuals to greater predation risk than when they foraged in the center of large patches (e.g. Suhonen 1993; Kotler et al. 2004; Carrascal and Alonso 2006). Head-up alertness is an important component of the vigilance response to threats of predation risk, allowing animals to better detect and respond to predators.

Results for some, but not all, of the other measures of vigilance behavior also support the hypothesis that birds use both indirect and direct cues to evaluate predation risk. Birds responded more strongly to direct cues of predation risk while foraging in small patches, than in the center of large patches. Head-turn frequency increased significantly in response to the predator compared to the non-predator call for birds foraging in small patches, but not for birds in the other two locations. Additionally, the change in head-turn frequency in response to the predator call was greater in small patches than in the center of large patches. Several studies have shown that head-turn frequency is highest for birds foraging alone, when they are at greatest risk of predation, and decreases in larger flocks (Lazarus 1979; Franklin and Lima 2001). Head-turning has been suggested as an important component of the vigilance response to predation risk and could have several anti-predator functions. First, head turns may be a predator

deterrent by informing the predator it has been detected and that the prey bird is alert (Woodland et al. 1980; Hasson 1991; Caro 1995). In birds, lateral movements of the head are also important for object and pattern recognition (Dawkins and Woodington 2000; Dittrich and Lea 2001) and might therefore play an important role in identification of an animal as a potential predator and threat. Head turns may also increase the effectiveness of head-up vigilance bouts by increasing the area of the environment scanned and allowing birds to better judge distances (Jones et al. 2007).

Birds foraging in the riskier small patches also increased the duration of head-up bouts in response to the predator compared to the non-predator call. Additionally, the change in head-up duration in response to the predator call was greater in small patches compared to the center of large patches. However, neither feeder location nor playback treatment influenced the frequency of head-up bouts. Thus the increase in time spent alert after the predator playback was likely due to an increase in the duration, not the rate, of head-up bouts. The potential cost of increasing head-up duration is a decrease in feeding rate (Fritz et al. 2002). For birds in this study, head-up frequency was likely correlated with food intake, because when the birds' heads were down, they were taking bites of food on the feeders. Thus if birds were trying to maintain their food intake rate post-playback, then head-up frequency would have increased (Cresswell et al. 2003). Instead, birds increased head-up duration at the cost of food intake, which could potentially have a negative effect on individual fitness. An increase in head-up bout duration may allow for a more effective assessment of the environment and could therefore be useful in situations when predators are known to be present (Glück 1987), such as after a direct cue of predator presence. Other studies have found that birds

increased their head-up duration at the expense of food consumption when indirect cues (foraging in visually obstructing habitats) indicate greater risk of predation (Elgar 1989; Whittingham et al. 2004).

Rather than responding to the threat of predation by immediately fleeing, birds in the more risky locations increased their vigilance. This response is aligned with optimal escape theory, which predicts that prey tolerate higher predation risk when food is present due to the potential loss of feeding opportunities if they flee upon immediately detecting a threat (Ydenberg and Dill 1986; Cooper 2003). Research on lizards shows that, when approached by a predator, individuals wait longer to flee if food is present than when it is absent (Cooper 2003) and when the quantity of food is high than when it is low (Cooper et al. 2006). Thus birds in this study may have responded to a cue of predator presence by increasing vigilance, rather than expending energy to flee and potentially losing the opportunity to continue foraging at a known, plentiful food source.

Small patches of forest habitat are common in tropical landscapes due to severe degradation and conversion to agriculture (Gaston et al. 2003). Additionally, forest restoration efforts are increasingly planting seedlings in small patches of tens to a few hundred metres squared as a cost-effective alternative to planting over large areas (Zahawi and Augspurger 2006; Rey Benayas et al. 2008). However, in choosing a restoration design, it is important to balance economic benefits with ecological consequences. Results from this study suggest that patch size can have a significant affect on vigilance behavior that could result in potential fitness costs to birds (Lima and Dill 1990; Cimprich et al. 2005; Carrascal and Alonso 2006). Thus forest restoration efforts using a patch-based planting scheme should consider that patch size is likely to

affect the quality of the patches as habitat for birds.

## CHAPTER 4

### BIRD AND BAT EFFECTS ON ARTHROPOD ABUNDANCES AND LEAF DAMAGE IN TROPICAL RESTORATION SITES

#### INTRODUCTION

Planting native vegetation is an increasingly common method to restore degraded lands (Jansen 2005). In tropical forest restoration projects, the growth and survival of planted trees is critical to restoration success (Holl et al. 2000). One potential obstacle to the success of restoration projects is the negative effects of herbivorous insects on planted vegetation. Herbivorous arthropods cause significant leaf damage in the tropics, with rates ranging from 10-40% (Coley and Barone 1996). Resulting leaf damage can reduce the photosynthetic abilities of leaves (Zangrel et al. 2002), negatively affecting growth, and can increase the likelihood of mortality in saplings and seedlings (Clark and Clark 1985; Norghauer et al. 2006; Eichhorn et al. 2010).

The top-down limitation of herbivorous insects by predators is an important ecological function that could facilitate growth of vegetation planted for restoration. Insectivorous birds can significantly reduce numbers of their insect prey (e.g., Holmes et al. 1979; Marquis and Whelan 1994). Birds have been shown to reduce herbivorous arthropod densities and their damage to plants in temperate forests (Marquis and Whelan 1994; Murakami and Nakano 2000; Strong et al. 2000), neotropical forests (Van Bael et al. 2003; Van Bael and Brawn 2005), and neotropical agroecosystems (Greenberg et al. 2000; Mols and Visser 2002; Van Bael et al. 2007). However, the relative effects of predators on arthropods and leaf damage in restoration systems has

not been investigated, despite the importance of vegetation growth and survival for the success of restoration projects.

Past research on the role of insectivorous birds in ecosystems has used exclosure experiments, where plants or branches are covered in netting, to show that avian insectivores influence the abundance of arthropod herbivores and levels of damage to plants. These studies have attributed all insectivory to birds, although exclosures were in place 24 hours a day (e.g. Greenberg et al. 2000; Van Bael et al. 2003; Boege and Marquis 2006; Koh 2008). In these cases, insectivory that was attributed to birds could have also included effects of bat insectivory. Bats are likely to play a significant role as predators of herbivorous arthropods, because many herbivorous arthropods in the tropics are active mainly at night and hide during the day (Kalka and Kalko 2006). Both foliage-gleaning bats (Subfamily Phyllostominae) and insectivorous birds consume arthropods in similar size-ranges (~4-30mm) and from similar taxa (LaVal and LaVal 1980). Bats also can consume large quantities of arthropods: gleaning bats consume over half of their body mass in arthropods nightly (Kalka and Kalko 2006).

Two recent studies have distinguished bird and bat predation. Both bird and bat predation reduced arthropod abundances, but not leaf damage, in a Mexican shade coffee system (Williams-Guillén et al. 2008). In the tropical forest understory of Barro Colorado Island, Panama, birds and bats reduced arthropods and leaf damage levels (Kalka et al. 2008). The relative role of birds and bats were different in these two systems: bat predation exceeded that of birds in the forest understory, while in the



coffee plantation, bird predation exceeded that of bats during the dry season, but the pattern was reversed during the wet season.

We used an exclosure experiment to examine the top-down effects of birds and bats on arthropods and leaf damage due to herbivory in restoration sites. Our study site is a large-scale restoration project where trees were planted in two different experimental treatments: islands, where several small patches of trees were planted and plantations, where trees were planted in one large patch to create continuous canopy cover. Thus we also investigated whether there were differences in the effects of bird and bat predation between the smaller patches found in the island treatment and the larger patch size of the plantation treatment.

We predicted that arthropod densities and leaf damage levels would be lowest on tree branches exposed to both bird and bat predation and highest on branches where both birds and bats were prevented from foraging. Although many species of foliage-gleaning birds are commonly detected in the restoration sites (Lindell et al. unpubl. data), we have little data on the use of the restoration sites by foliage-gleaning bats. Additionally, previous work on the relative effects of birds and bats has been variable (Williams-Guillén et al. 2008; Kalka et al. 2008). Thus we did not have any predictions for which predator might have stronger effects on arthropods and leaf damage. Birds, and potentially bats, are less likely to visit small than large patches (Zahawi and Augspurger 2006; Fink et al. 2008; Schulze et al. 2000; Bernard and Fenton 2003). Thus we predicted that differences in arthropods and leaf damage levels between branches that excluded both birds and bats and branches with no exclosures would be greater in

larger patches, where birds and bats are more likely to be found, than branches in smaller patches.

## METHODS

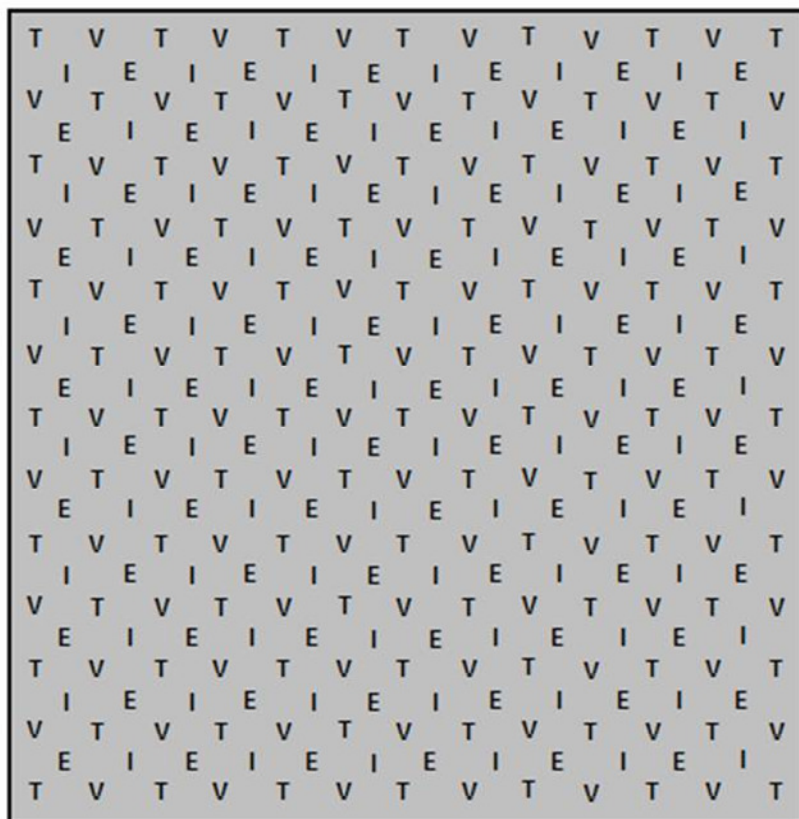
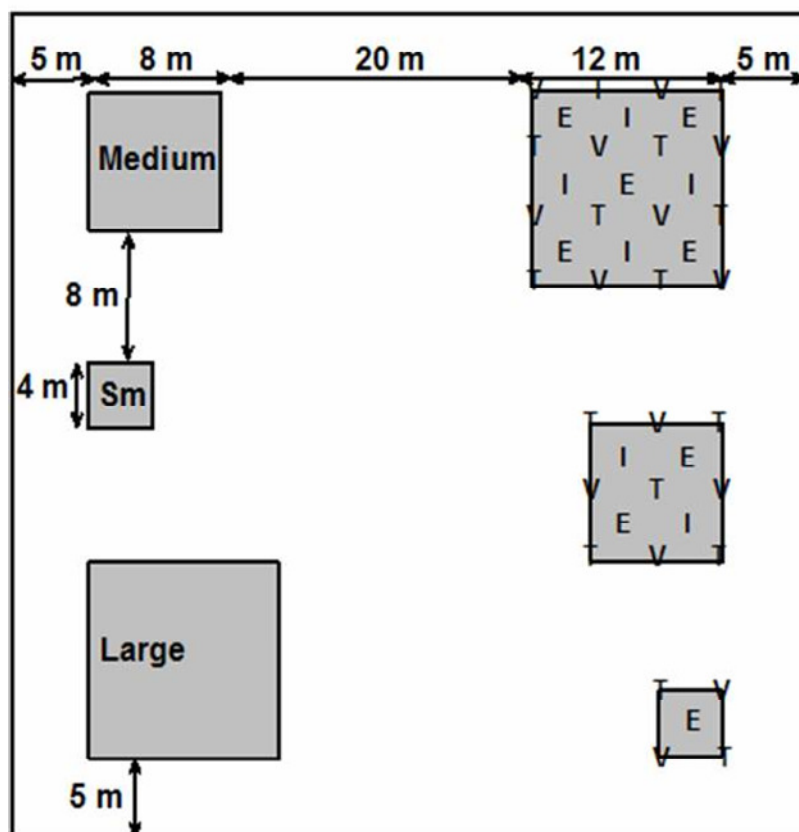
*Sites and Location:* The study was conducted from June to July 2009 in four restoration sites located near the town of Agua Buena (8° 44' N, 82° 58' W; elevation 1100-1300 m) in southern Costa Rica. One site was planted in 2004 and the other three in 2005. All sites were at least 3 km apart. All restoration sites had previously been used for ≥18 years for agriculture (Cole et al. 2010). In the past 50 years most land surrounding Agua Buena was cleared for agricultural use, primarily for the production of sun coffee with some land used for pasture and subsistence agriculture. Currently, less than 27% of the original forest remains in the region, mostly in small riparian fragments or on mountains at higher elevations. The landscape surrounding the restoration sites is dominated by pasture, sparsely-shaded coffee and other agriculture, small human settlements and some patches of secondary and mature Pacific premontane humid forest (Daily et al. 2001; Sekercioglu et al. 2007).

The restoration sites were planted with four seedling species: *Terminalia amazonia* (J.F. Gmel.) Exell [Combretaceae], *Vochysia guatemalensis* Donn. Sm. [Vochysiaceae], *Erythrina poeppigiana* (Walp.) O.F. Cook [Fabaceae], and *Inga edulis* Mart. [Fabaceae]. All species are native or naturalized to the region and are widely used in tropical forest restoration (Nichols et al. 2001; Carpenter et al 2004).

We used two experimental treatments at each site. Treatment plots were 50 x 50 m and either had (1) trees planted in rows to cover the entire plot (plantation, 2500 m<sup>2</sup>),

or (2) trees planted in six patches of three different sizes (Figure 4.1). Vegetation was cleared around planted trees every 2-3 months for the first two and a half years after planting to allow seedlings to become established. The small number of seedlings that died during this time were replanted. No further clearing or planting was conducted after January 2007. Tree heights ranged from 3-9 m in 2008. Plantation plots had an almost continuous canopy over the 50 x 50 m treatment area. The large, medium and small patches within the island plots remained distinct patches within a matrix of herbaceous vegetation.

Figure 4.1: Planting arrangement at each restoration site. Each site had one 50 x 50 m extra-large patch (bottom) and one 50 x 50 treatment with six smaller patches (top): two large (12x12 m), two medium (8x8 m) and two small (4x4 m). Each side of the second treatment had one small, one medium and one large patch, although the arrangement of the patches varied among sites. The number and arrangement of the tree species within the patches was constant across all sites. Shaded areas are planted with trees. Tree species are indicated by letters: *Erythrina* (E), *Vochysia* (V), *Inga* (I), and *Terminalia* (T). Non shaded areas are non-woody vegetation, primarily grasses. Sm=small patch.



Although the number of seedlings planted in each plot was initially the same, seedling growth and mortality varied, resulting in variation in canopy cover among patch sizes and tree species. Thus we measured island and plantation size by measuring canopy cover for every tree in the medium and large islands and one-third of the trees (selected at random) in each plantation. To measure individual tree canopy cover, we used the formula for the area of an ellipse ( $\pi d_1 d_2 / 4$ ); where  $d_1$  = the longest canopy diameter and  $d_2$  = the diameter perpendicular to  $d_1$ . To calculate total canopy cover for each island, we summed the canopy cover of all trees within each island. For plantations, we multiplied the average canopy cover of each tree species by the number of each species in that patch (Fink et al. 2009).

Exclosures: The experiment was conducted during the Costa Rican wet season, from 31 May - 2 July 2009 (33 days) at two of the four sites and from 6 July - 7 August 2009 (33 days) on the other two sites. We conducted the exclosure experiments using *Inga edulis* trees only. *Inga* trees had the greatest canopy cover in the restoration sites and were the most commonly used trees by foraging birds in 2007 and 2008 (Fink et al. 2009; Morrison et al. unpubl data).

Exclosures were placed in a total of 30 *Inga* trees in the plantation (between 7-8 trees per plantation). Due to logistical constraints, we only used nine patches in the island treatment, with a total of 16 *Inga* trees used for exclosures (between 1-4 *Inga* trees per island). The total canopy cover of the four plantations treatments ranged from 1659.3 - 3139.4 m<sup>2</sup>, and the total canopy cover of the nine different islands of the island treatment ranged from 101.0 - 352.0 m<sup>2</sup>.

The *Inga* from the plantation treatment were randomly selected from those individuals that were within 5 m of the edge of the plantation to control for distance to edge (*Ingas* in the islands were within 5 m of the edge of the island). On each tree we selected four branches: one control branch (no exclosure, both birds and bats present), one bat-only exclosure branch (exclosure at night only, birds present), one bird-only exclosure branch (exclosure during the day only, bats present) and one bird+bat exclosure branch (exclosure was in place during both day and night, neither birds nor bats present). Branches were located between 1-2.5 m off the ground and were located on the outer edge of the tree. Exclosures were constructed around an approximately 0.75 m-length of branch, using agricultural netting (mesh opening 2 x 2 cm; Van Bael et al. 2003; Kalka et al. 2008; Williams-Guillén et al. 2008). Exclosures restricted access by birds and bats but allowed access by arthropods, including spiders and large Lepidoptera larvae (Morrison pers. obs.)

Each day during the experimental period, exclosures were placed on bat excluded branches at dusk and removed at dawn, while exclosures were placed on bird excluded branches at dawn and removed at dusk. Control branches had no exclosure for the duration of the experiment. Exclosures on bird+bat branches were left in place for the duration of the experiment.

*Arthropod and Leaf damage Census:* Arthropods were visually censused on all experimental branches two days before the exclosures were placed on the branches and then once weekly thereafter for four weeks (Kalka et al. 2008; Williams-Guillén et al. 2008). All arthropods were categorized into 1 mm size intervals and identified to at least the order level: Aranae, Orthoptera, Dermaptera, Hemiptera, Homoptera,

Coleoptera, Lepidoptera adults, Lepidoptera larvae, Diptera, Formicidae and other Hymenoptera (bees and wasps), unknown adults, and unknown larvae. Length-weight regressions from Johnson and Strong (2000) and Schoener (1980) were used to calculate arthropod biomass for all Orders.

Only some arthropod orders are herbivorous (chewing insects). These include Coleoptera, Orthoptera, Dermaptera and larvae from Lepidoptera or Coleoptera. Other orders are sucking insects that feed on plant phloem, prey on other arthropods, or are in feeding guilds other than herbivores. Thus we only used the chewing insects orders to calculate arthropod biomass.

In order to standardize arthropod data for leaf area, we created a regression equation by measuring the lengths, widths and areas for 200 leaves (50 leaves taken from each of the four sites). We then measured the length and width of all leaves on each exclosure branch and used the regression equation to estimate the total leaf area of all leaves for each exclosure. By using the regression equation we did not have to destructively sample leaves in the exclosures. Measures of arthropod abundance were then expressed as insect mg/leaf m<sup>2</sup> for each exclosure. Leaf length and width measurements were taken immediately before the exclosures were set up.

Leaf damage due to herbivory was assessed at the end of the experiment and was measured only on new leaves that flushed after the experiment began (Van Bael et al 2003; Van Bael and Brawn 2005). We took digital photographs of these leaves and used the software ImageJ v1.43 (National Institutes of Health, USA) to measure the proportion of the leaf that was missing. Thus our measure of leaf damage included only missing leaf tissue that was assumed to be from herbivorous insects, not other damage



(such as texture changes due to fungi or viruses). Estimates of leaf damage from this study are likely conservative, because we did not take into account the effects of leaf mining (brown spots due to sucking insects). Evidence of fungi or viruses on leaves was rare.

*Data Analysis:* We measured the effects of plot type (island or plantation) and treatment (both birds and bats present, birds only present, bats only present, neither birds or bats present) on arthropod abundance (arthropod mass/leaf area) using repeated measures mixed effects models. The four insect sampling periods were the repeated within-subject factor, and treatment, plot and the treatment by plot interaction were between-subject factors. Site was included as a random factor. Sampling period (June or July) was initially included as a fixed factor, but was not significant, likely because it was correlated with the effects of site. We initially included the patch size (measured as m<sup>2</sup> of canopy cover, see above) of each plantation and island patch in the model, but this variable was not significant and was removed from subsequent analysis. We used interaction contrasts to do pairwise comparisons of the effects of exclosure treatment on arthropod abundance in the island and plantation locations.

We used linear mixed effects models to examine the fixed effects of plot type (island or plantation), treatment, and the interaction between plot and treatment on proportion of leaf damage. Site was included as a random factor. As above, sampling period and patch size were not significant factors in the models and were removed from subsequent analyses. We used interaction contrasts to do pairwise comparisons of the effects of exclosure treatment on proportion leaf damage in the island and plantation locations.

All analyses were conducted using SAS v9.1 (SAS Institute, Inc.). All variables were examined for normality and homoscedasticity and proportion leaf damage and arthropod biomass (arthropod mass /leaf area) were square root transformed. Differences between groups were considered significant when  $P < 0.05$ .

## RESULTS

### *Pre-exclosure arthropod biomass*

Arthropod biomasses measured before the start of the exclosure experiment did not vary significantly different among the branches used for experimental treatments ( $F_{3,168} = 0.76$ ,  $P = 0.52$ ) nor did they differ between islands and plantations ( $F_{1,169} = 3.09$ ,  $P = 0.08$ ). The plot by treatment interaction was not significant ( $F_{3,168} = 0.44$ ,  $P = 0.72$ ).

### *Arthropod biomass*

Arthropod biomass was significantly affected by exclosure treatment ( $F_{3,716} = 23.2$ ,  $P < 0.001$ ), but not different between islands and plantations ( $F_{1,717} = 0.11$ ,  $P = 0.74$ ; Figure 4.2). The interaction between exclosure and planting treatments was not significant ( $F_{3,716} = 1.33$ ,  $P = 0.26$ ).

In both the island and plantation treatments, branches where both birds and bats were excluded (no predators present) had significantly higher arthropod biomass than branches where both predators were present (no exclosure), branches where only birds were present (bat-excluded) and branches where only bats were present (bird-excluded) (all  $P \leq 0.02$ ; Figure 4.2). Arthropod biomasses on bat-only and bird-only branches did not differ significantly from one another in either islands ( $P = 0.89$ ) or plantations ( $P = 0.13$ ; Figure 4.2). In the islands, both bat-only and bird-only branches

had significantly higher arthropod biomass than branches where both were present (all  $P \leq 0.01$ ; Figure 4.2). However in the plantations, only bird-only branches had significantly greater biomass than the branches where both were present ( $P < 0.01$ ; Figure 4.2).

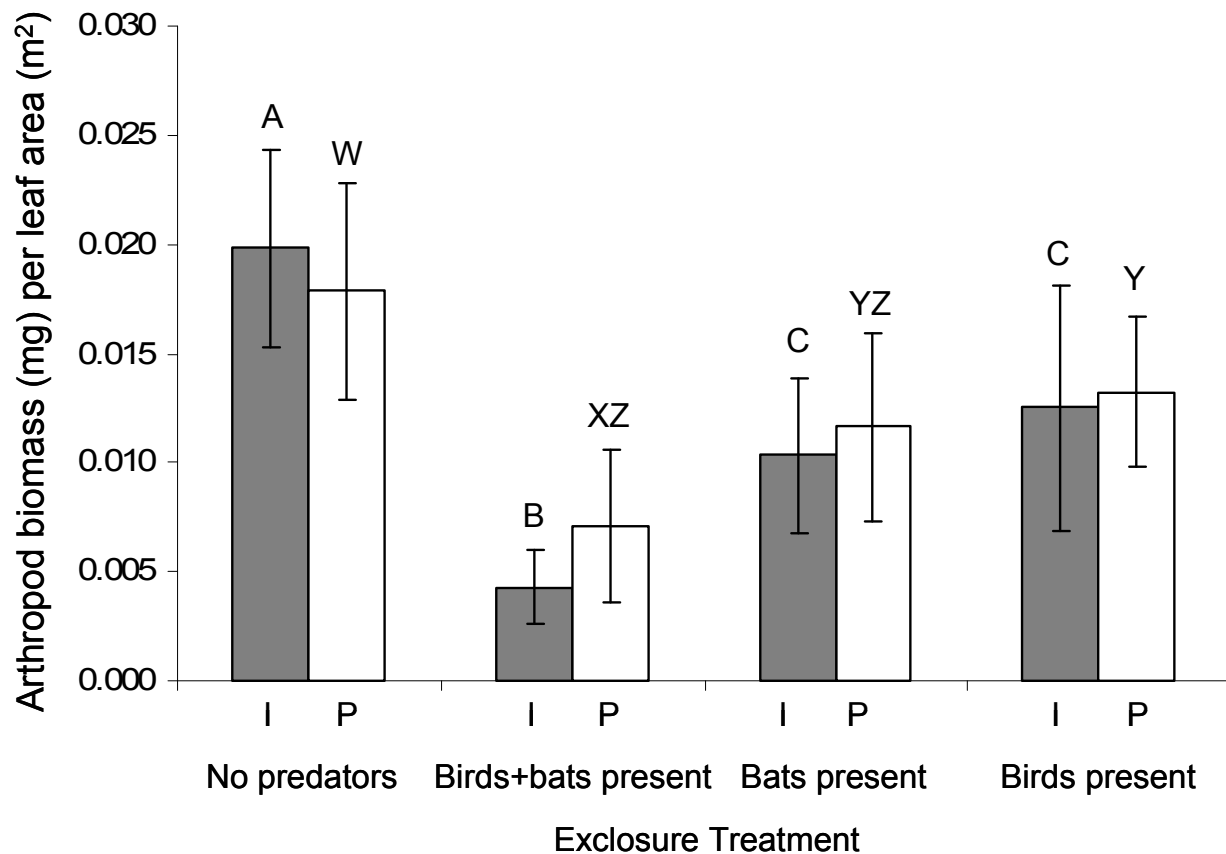
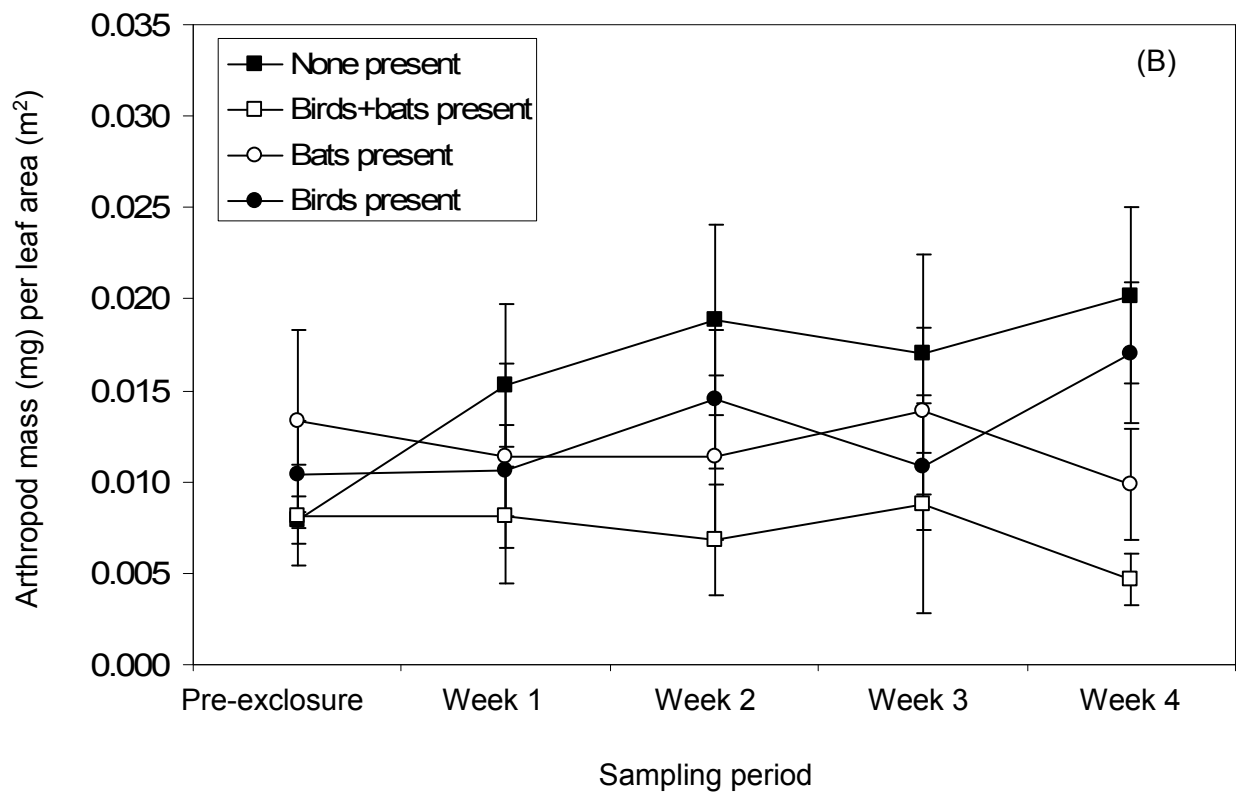
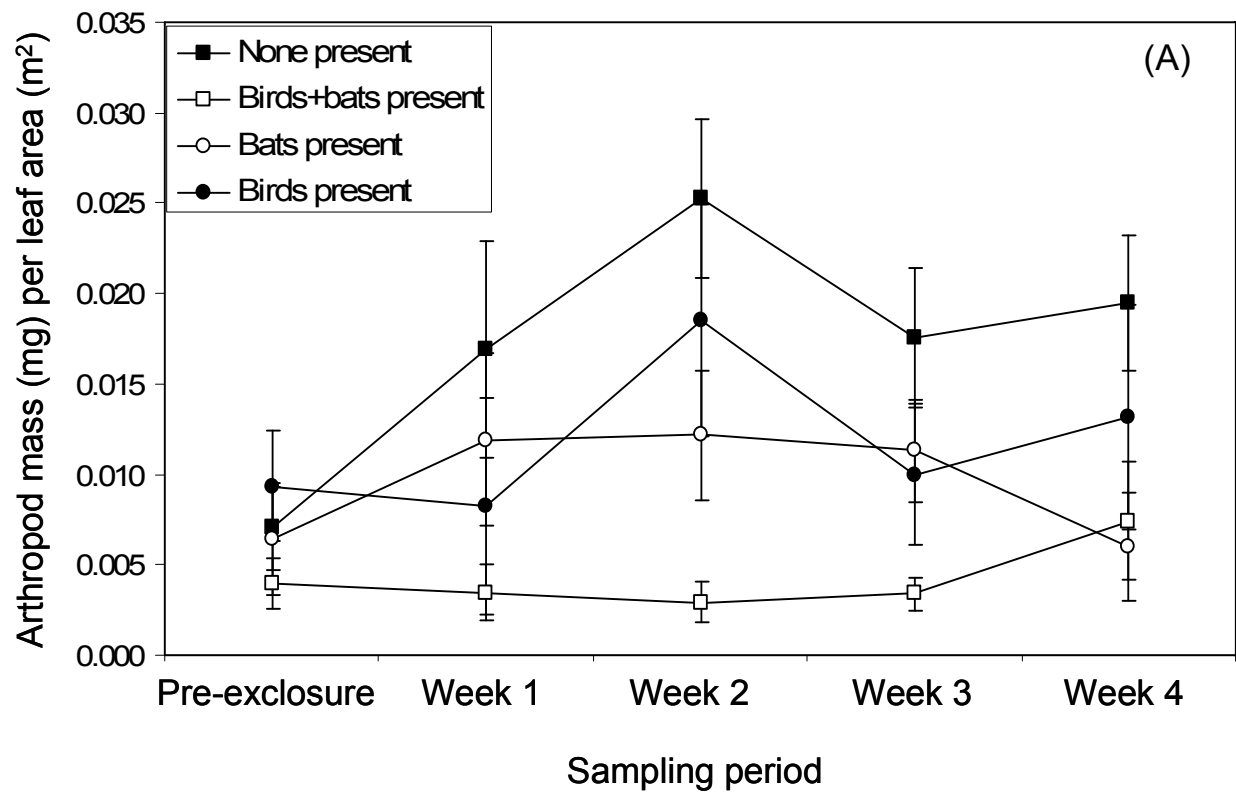


Figure 4.2: Data from islands and plantations showing average arthropod biomass (mg of arthropods/leaf area m<sup>2</sup>) per census in each of the four exclusion treatments. None present = exclusion 24-hrs, excluded both birds and bats, Birds+bats present = no exclusion, neither birds nor bats excluded, Bats present = birds only excluded, bats present, Birds present = bats only excluded, birds present. Different letters represent significant pairwise ( $P < 0.05$ ) differences based on post-hoc tests from the repeated measures mixed effect model. There were no significant pairwise differences in leaf damage between islands and plantations within any of the four exclusion treatments. The letters A-D are for the island treatment only, and the letters W-Z are for the plantations treatment. Standard error bars are shown.

Arthropod biomass on branches where both birds and bats were present remained relatively consistent across all sampling points for both islands and plantations, while arthropod biomass increased on branches where both birds and bats were excluded after the first few sampling periods (Figures 4.3a-b). Arthropod biomass for bird-only and bat-only branches also increased, but at an intermediate level compared to the other treatments (Figures 4.3a-b).

Figure 4.3. Variation in arthropod biomass over the five sampling periods in the islands (A) and plantations (B). Pre-exclosure measurements were taken two days before the experiment began. Each of the other samples were taken once weekly thereafter for four weeks. None present = exclosure 24-hrs, excluded both birds and bats, Birds+bats present = no exclosure, neither birds nor bats excluded, Bats present = birds only excluded, bats present, Birds present = bats only excluded, birds present. Standard error bars are shown.



*Leaf damage due to herbivory*

Both exclosure treatment ( $F_{3,173} = 3.28$ ,  $P = 0.02$ ) and planting treatment ( $F_{1,174} = 7.03$ ,  $P = 0.001$ ) had significant effects on leaf damage. The interaction between exclosure and planting treatment was not significant ( $F_{3,173} = 0.46$ ,  $P = 0.71$ ).

Proportion of leaf damage across all exclosure treatments was higher in the plantations ( $0.158 \pm 0.009$ ) than in the islands ( $0.125 \pm 0.013$ ;  $P = 0.01$ ). However, within each exclosure treatment, there were no significant pairwise differences in leaf damage between islands and plantations (all  $P \geq 0.31$ ; Figure 4.4). In the islands, leaf damage did not differ between the four treatments (all  $P \geq 0.09$ ; Figure 4.4). In the plantations, however, leaf damage due to herbivory was significantly higher on the branches where both birds and bats were excluded compared to each of the other three treatments ( $P \leq 0.02$ ; Figure 4.4).

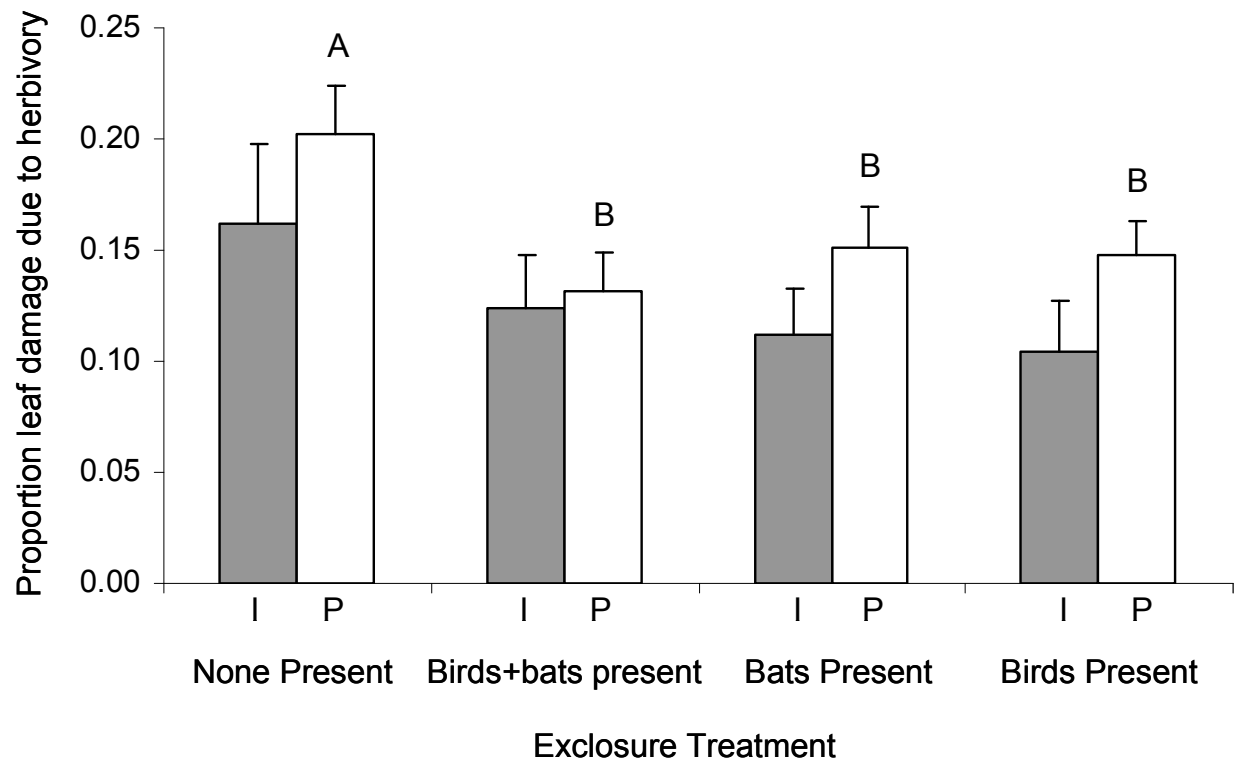


Figure 4.4: Proportion damage due to herbivory for leaves in the four exclusion treatments within the two planting treatments (Island and Plantation). None present = exclusion 24-hrs, excluded both birds and bats, Birds+bats present = no exclusion, neither birds nor bats excluded, Bats present = birds only excluded, bats present, Birds present = bats only excluded, birds present. Different letters represent significant pairwise ( $P < 0.05$ ) differences based on post-hoc tests from the linear mixed effect model. There were no significant pairwise differences in leaf damage between islands and plantations within any of the four exclusion treatments. Standard error bars are shown.

## DISCUSSION

Foraging by both birds and bats had a significant impact on arthropod populations and, in plantations these effects translated to lower levels of leaf damage. In island and plantation patches combined, arthropod biomass on branches where both predators were present was 70% lower than that observed on branches where both predators were excluded. Leaf damage due to herbivory was 32% lower on branches



where birds and bats were present compared to branches where they were both excluded.

When either birds or bats were present, arthropod biomass was lower than when both were excluded and higher than when both were allowed access to branches. However, our data show that the effects of birds and bats on the populations of herbivorous insects are approximately equivalent in this system. This result differs from the few other studies that have examined the relative differences between top-down effects of bird and bat in tropical systems. Both bird and bat predation reduced arthropod abundances in a Mexican shade coffee system, but the effect of bird predation exceeded that of bats in the dry season, while the effect of bats exceeded that of birds in the wet season (Williams-Guillén et al. 2008). In the tropical forest understory of Barro Colorado Island, Panama, birds and bats reduced arthropods, however the effect of bat predation exceeded that of birds (Kalka et al. 2008).

Restoration planting treatment, island (small patches) or plantation (large patches), had no significant effect on the impact of birds and bats on arthropod biomass, but did affect levels of leaf damage due to herbivory. In islands, no significant differences in leaf damage between exclosure treatments were detected, but in plantations, leaf damage levels were higher on branches where birds and bats were excluded than on branches where both had access. However, neither predator by itself was able to reduce leaf damage compared to control branches where both were excluded. Birds and bats are clearly removing some of the population of herbivorous arthropods, but the indirect effect of their consumption did not translate into strong reduction of herbivore damage to leaves. Williams-Guillén et al. (2008) also found no

effects of birds or bats on leaf damage levels in coffee plantations, despite clear effects of each predator on arthropod populations.

The few studies that have examined the top-down effects of bird and bat insectivory show that the relative effects of birds and bats vary across habitat type and season. There are several potential mechanisms that could explain these differences. First, food chain theory suggests that trophic cascades will be strongest when and where plant productivity is highest (Fretwell 1977; Oksanen et al. 1981; Van Bael and Brawn 2005). Results from a tropical forest in Panama show that the effects of bird predation on arthropods and leaf damage were strongest at locations where, and during the times of year when, the highest level of leaf production occurred: during the wet season, compared to the dry season, and in forest canopies, compared to the understories (Van Bael and Brawn 2008).

Kalka et al. (2008) found that bats, and to a lesser extent birds, had strong effects on reducing arthropods and leaf damage during the wet season, when plant productivity is predicted to be highest. In contrast to trophic theory, however, these strong trophic cascades were found on understory plants, a location predicted to have low plant productivity. Birds and bats were also found to reduce arthropods, but not herbivory, on understory coffee plants shaded by a taller overstory canopy (Williams-Guillén et al. 2008). However, birds and bats had differing effects in the coffee agroecosystem that were dependent on season (Williams-Guillen et al. 2008). The present study was also conducted during the wet season, when arthropod herbivore populations peak in response to new leaf production (Barone 1998; Wolda 1978), and theory suggests that trophic cascades should be strongest. Although the relative impact

of bird and bat insectivory in the restoration sites resulted in detectable differences in arthropod biomass among exclosure treatments, this did not translate into strong effects on leaf damage. Plant productivity was not measured in any of these three studies, so it is unknown how actual leaf production rates affected these results.

Other seasonally dependent events could also affect the strength of these trophic cascades. In the neotropics, the wet season also corresponds to the nesting season for many insectivorous birds, which have an increased demand for arthropods to feed their young (Martin 1987). On the other hand, during the dry season, the neotropics experience an influx of millions of overwintering migratory birds that could also affect arthropod populations (Greenberg 1995; Jedlicka et al. 2006).

These recent studies on the relative effects of birds and bats on controlling arthropod populations and leaf damage suggest that the relationships among trophic levels in these ecosystems is complex and dependent on a number of different factors including density and types of bird, bat and plant species present, the structure of the habitat and variation in abiotic factors due to season. More studies are needed to examine the exact nature of these trophic interactions. Additionally, information on the habitat use, densities, foraging behavior and diet of tropical insectivorous birds is understudied, and this information is extremely limited for bats (Kalka and Kalko 2006).

We likely underestimated the effects of birds' and bats' insectivory on leaf damage. Leaf damage due to arthropods potentially extends beyond the phytophagous guilds we studied here, to insect that consume plant phloem. Phloem-feeding insects can also damage plants, leading to reduced photosynthetic ability, growth and survival (Goggin 2007). Birds and bats may also have reduced the impact of phloem-feeders in

this study, however damage due to these insects is much more difficult to measure. Also, recent work has shown that measuring holes in leaves, as in this study, may significantly underestimate the actual damage caused by chewing arthropods (Zangerl et al 2002). The leaf areas directly adjacent to holes left by herbivorous arthropods suffers reduced photosynthetic ability and can cover an area larger than the area directly damaged by leaf consumption. Thus it is likely that birds and bats are having greater direct and indirect effects on arthropods and plants than what we could measure in this study.

Previous research has established that some groups of birds and bats have important ecological roles as seed-dispersers in restoration systems (Bianconi et al. 2007; Cole et al. 2010), but their roles as insect predators was previously unknown. Our data show that these two top predators in tropical restoration systems can impact arthropod populations. Our data also suggest that resulting indirect effects of bird and bat insectivory on leaf damage, an important influence on plant growth and survival, were strongly dependent on the presence of both predators. Studies that have examined trophic cascades have suggested that the presence of predators can have important effects on forest productivity, and this effect could also be important to restoration success (Marquis and Whelan 1994; Terborgh et al. 2001). Thus restoration efforts should emphasize the importance of attracting top predators communities, rather than one or a few species, in order to establish crucial trophic processes important for ecosystem function (Terborgh et al. 2001).

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