Title
Restoring birds, bats, and dispersal mutualisms in a tropical, agricultural landscape

Author
Reid, John Leighton

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RESTORING BIRDS, BATS, AND DISPERSAL MUTUALISMS IN A TROPICAL AGRICULTURAL LANDSCAPE

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by

John Leighton Reid

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The dissertation of John Leighton Reid is approved:

Professor Karen Holl, chair

Professor Gregory Gilbert

Associate professor Flora Lu

Rakan Zahawi, Ph.D.

Professor emeritus Theodore Fleming

Tyrus Miller
Vice Provost and Dean of Graduate Studies

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Abstract

Restoring birds, bats, and dispersal mutualisms in a tropical agricultural landscape

J. Leighton Reid

Ecological restoration is an aggressive response to ongoing tropical deforestation, which continues to disarticulate the world's most diverse terrestrial communities, undermine rural livelihoods, and exacerbate anthropogenic climate change. Here I use three approaches to address the question: How and where can we best restore tropical biodiversity? I focus on birds and bats – important beneficiaries and benefactors of forest restoration – and on the restoration of degraded pastures in southern Costa Rica. First, I evaluate impacts of local restoration treatments and landscape context on bird communities in an replicated experiment. I find that high-intensity restoration plantings improve old-growth bird biodiversity and community attributes of three functional groups that mediate biotic barriers to forest succession. Restoration has the greatest capacity for conserving old-growth bird species when projects are situated within largely intact forested landscapes, suggesting that one means of safeguarding biodiversity through restoration could be to preferentially allocate funding to such regions. Second, I test the efficacy of artificial bat roosts as a novel strategy to accelerate forest recovery. The premise is that provisioning simulated tree cavities may attract bats into abandoned pastures where they will disperse seeds and create patches of regenerating vegetation. During a two-year study, bats rarely used roosts in pastures, and increased seed rain below roosts did not translate into increased seedling recruitment. This work underscores the general importance of addressing post-dispersal limitations on seedling recruitment in restoration. Third, I explicitly address the importance of human behavior by applying a conservation psychology approach to the question: Why do some Costa Ricans kill roosting bats? Using qualitative and quantitative methods, I find that bat killing is common among men in Coto Brus County and that natural history knowledge and negative experiences with vampire bats (*Desmodus rotundus*) are important predictors of relevant beliefs about bat killing. These results suggest that environmental education and mitigation of damage to livestock by vampire bats are important components of regional bat conservation. Moreover, this conservation psychology approach is likely to be applicable to a wide range of conservation problems.

This dissertation is dedicated to my parents,

Jim and Cindy Reid,

for their love and encouragement.

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1. Introduction

Tropical forests are the most diverse terrestrial ecosystems on Earth. Out of an estimated global diversity of 8.7 ± 1.3 million Eukaryotic species (Mora et al. 2011), it is likely that at least half live in tropical forests despite the fact that these forests historically occupied only ~13% of the Earth's land surface (Wilson 1992, Olson et al. 2001). Tropical forests also sustain and enrich humanity. Many people use forests as sources of food, fuel, building materials, medicine, and clean drinking water (Byron and Arnold 1999), and tropical forests also represent an important carbon sink that buffers global climate change (Pan et al. 2011).

Despite their importance, tropical forests continue to be cleared at an alarming rate. Between 2000 and 2005, ~27 million ha of tropical forest were cleared, representing ~1.4% of the entire biome (Hansen et al. 2008). Three-fifths of this deforestation occurred in Latin America, and while the past eight years have seen significant improvements (e.g., reduced clearing in the Brazilian Amazon; Nepstad et al. 2009), deforestation is still a dominant regional land-use change (Aide et al. 2012). This ongoing deforestation is disarticulating the world's most diverse ecosystems, undermining rural livelihoods , and exacerbating global climate change (Brook et al. 2003, Fearnside 2005, Chhatre and Agrawal 2009, Gibson et al. 2011). Deforestation also accounts for 12-15% of anthropogenic carbon emissions, making it the second largest greenhouse gas source after fossil fuel combustion (IPCC 2007, van der Werf et al. 2009).

Ecological restoration is an aggressive response to mitigate these negative consequences. The Society for Ecological Restoration (2004) defines restoration as "...an intentional activity that initiates or accelerates the recovery of an ecosystem with respect to its health, integrity, and stability." The basic premise of restoration is that for some cost (*i.e.*, time, effort, or money), a degraded ecosystem can be returned to a state that is more like the ecosystem that was present historically (*i.e.*, in structure, function, and composition). Complete restoration, however, is rarely achieved due to irreversible changes (*e.g.*, invasive species), hysteresis, and uncertainty surrounding historic baselines (Hobbs and Suding 2009, Jackson and Hobbs 2009, Hobbs et al. 2011). Moreover, the relative success of restoration effects is highly variable in space and time (Chazdon 2008, Holl and Aide 2011). A fundamental question is therefore *how and where can ecosystems best be restored?*

In this dissertation I address this question using the restoration of tropical forest on abandoned cattle pastures as a model system. Cattle pastures are a focal point in tropical forest restoration literature because they are inexpensive and ubiquitous - commonly representing an endpoint in the chain of degradation following forest clearing (Holl and Kappelle 1999). From a theoretical perspective, cattle pastures are also an interesting model system because their restoration entails the conversion of an extremely simple ecosystem to one of the world's most complex. Secondary succession in tropical pastures is limited by a suite of factors which can be summarized as a lack of seed arrival and poor seedling survival (Aide and Cavelier 1994, Holl 1999, Reid and Holl 2012). Seed rain, particularly of animal-dispersed species, diminishes rapidly beyond forest edges (Holl et al. 2000, Cubiña and Aide 2001) because most frugivorous animals have little reason to venture into cattle pastures, which are hot, largely devoid of structure or food resources, and potentially dangerous. Seeds that do arrive have only a small chance of germinating and surviving (Aide and Cavelier 1994); one study estimated seed survival to be less than one in 100 over an 18-mo period (Holl 2002). Seed mortality is commonly due to predation, dessication, or rot (Cole 2009). Seedlings succumb to herbivory and competition with ruderal vegetation (Nepstad et al. 1990, Holl 1998).

Within the context of tropical forest restoration, my research has focused on animals, particularly birds and bats. Animals are clear beneficiaries of forest restoration. The greatest cause of animal endangerment is habitat loss (Dirzo and Raven 2003), and restoration directly affects this driver (Young 2000). Animals are also important benefactors of restoration, providing ecosystem functions that assist in overcoming barriers to secondary succession. Most tropical tree species are dispersed by vertebrate animals (Howe and Smallwood 1982), and frugivorous birds and bats are predominant seed dispersers in early-successional tropical habitats (Fleming 1988, Whittaker and Jones 1994, Galindo-Gonzalez et al. 2000, Ingle 2003, Muscarella and

Fleming 2007, Lindell et al. 2012). Insectivorous birds and bats also increase seedling survival and growth by reducing the abundance of herbivorous arthropods (Kalka et al. 2008, Morrison and Lindell 2012), and nectarivorous birds and bats contribute to the long-term sustainability of regenerating forests by maintaining gene flow through pollination (Sekercioglu 2006, Dixon 2009, Kunz et al. 2011).

The central question of this dissertation is how and where can tropical biodiversity best be restored? I have used three approaches to answer this question. All three of these studies were conducted in the agricultural landscape of Coto Brus, Costa Rica.

In Chapter 1, I report on the impacts of local restoration intensity and landscape context on bird communities in an experimentally-replicated restoration experiment. I demonstrate that high-intensity restoration plantings increase old-growth bird biodiversity and the abundance or richness of three functional groups (frugivores, nectarivores, migrant insectivores) that provision important ecosystem functions (seed dispersal, pollination, arthropod reduction). I also show that restoration will have the greatest positive effect for conserving old-growth bird biodiversity when restoration plots are situated within largely intact forested landscapes, but three functional groups respond similarly to restoration interventions anywhere in a heterogeneous landscape. This study provides novel data to inform sub-national prioritization frameworks for new restoration funds from programs such as the United Nations REDD+ (Reducing Emissions from Deforestation and forest Degradation).

Despite the fact that all restoration projects are spatially explicit and have variable results from site to site, experimental replication across landscapes has generally been rare due to implementation costs and logistical challenges. This chapter also provides insight on conservation applications of the Biodiversity-Ecosystem Function relationship, an active research topic in contemporary ecology.

In Chapter 2, I test a novel restoration strategy - using artificial bat roosts to accelerate tropical forest recovery. Novel restoration strategies are an important research area; the holy grail of forest restoration would be a technique that is accessible, inexpensive, and highly efficient. The premise of artificial bat roosts is that by provisioning a potentially limiting resource (roosting space in a simulated tree cavity) for bats, one can attract bats into abandoned pastures where they will disperse seeds and create patches of regenerating vegetation (Kelm et al. 2008). During my two-year study, bats readily used roosts in forests but not in pastures, and whereas seed rain abundance was higher below roosts that were used by fruit bats, seedling recruitment did not increase. Based on these observations, I conclude that bat roosts are unlikely to be a useful tool for forest restoration. This experiment will be useful for researchers and conservation practitioners who are already implementing or considering artificial roosts for forest restoration projects in Mexico, Nicaragua, Costa Rica, Colombia, and Brazil, and my results will hopefully help to prevent the misallocation of limited restoration funding to projects that are not likely to succeed.

In Chapter 3, I explicitly address the importance of human behavior in biodiversity conservation. Specifically, I use qualitative and quantitative social science methods to identify the psychological determinants for why some Costa Ricans kill roosting bats on their farms. I show that 14% of rural men in Coto Brus County have killed roosting bats over the preceding five years, and 27% intend to kill bats if they find them roosting on their farms. The most common negative belief that correlates with bat killing intentions is that killing bats helps reduce damage and disease transmission to livestock. Conversely, men who had pro-conservation attitudes generally believed that killing bats would reduce ecosystem services on their farms or be a detriment to nature. The best predictors of these key beliefs were natural history knowledge and exposure to livestock damage by vampire bats. This work supports the notion that environmental education is a useful tool for promoting pro-conservation behavior, but it also highlights that conservation strategies must address the risk that people face as a result of living with biodiversity. More generally, this chapter provides an empirical example of an analytical framework that may be useful for approaching other conservation questions involving quantitative human behaviors.

This work builds upon my previous research on bird habitat selection (Reid et al. 2008, Reid et al. 2012a), seed dispersal (Lindell et al. 2012, Reid et al. 2012b), and seedling recruitment (Reid and Holl 2012, Holl et al. 2013, Zahawi et al. 2013) in tropical forest restoration. Descriptions of my bat roost experiment have been published (Reid 2009b, Reid and Casallas-Pabón 2012). Forthcoming manuscripts aside from the research presented here will describe bat and seed rain communities in tropical forest restoration.

2. Landscape context mediates avian habitat choice in tropical forest restoration

2.1. Summary

Ecological restoration seeks to reverse the rapid loss of biodiversity and ecosystem function. Restoration projects are spatially explicit, but the cost of interventions has largely precluded experimental replication across landscapes. We addressed this gap using a uniquely well-replicated restoration experiment combined with hand-digitized tree cover to evaluate interactions between local restoration and landscape context for predicting avian composition and functional groups at 13 sites across a Neotropical landscape. Frugivore abundance, nectarivore abundance, migrant insectivore richness, and compositional similarity of bird communities to old-growth forest were each greater in tree plantations than in less intensive treatments. Frugivores, nectarivores, and old-growth similarity were correlated with landscape tree cover within site radii of 0.35-0.55 km, but migrant insectivores did not respond to tree cover at any scale. Bird communities increasingly resembled old-growth communities when tree plantations were embedded in landscapes with high tree cover, but frugivores and nectarivores were more abundant in intensively restored sites regardless of matrix composition. Discrepancy in landscape effects for functional groups and community composition suggest that trade-offs between biodiversity conservation and ecosystem functioning may be important when selecting restoration sites. We provide novel

prioritization criteria for allocation of reforestation funds from REDD+ at sub-national scales.

2.2. Introduction

Ecological restoration is the process of assisting the recovery of degraded ecosystems to their historic trajectories (SER (Society for Ecological Restoration) 2004). Interventions such as tree planting are effective for restoring biodiversity (*e.g.*, species diversity, abundances, or biomass) and ecosystem services (*e.g.*, nutrient cycling, soil stabilization, or climate regulation) in tropical terrestrial ecosystems (Rey Benayas et al. 2009). These restoration efforts help offset the impacts of ongoing deforestation (Redo et al. 2012) that threaten to exacerbate climate change and drive extinctions in the world's richest biological communities (Webb et al. 2006).

Restoration projects are spatially explicit, but rarely replicated across landscapes due to high implementation costs (Ruiz-Jaen and Aide 2005). As such, our understanding of the importance of landscape context on the recovery of communities and their associated ecosystem functions and societal benefits are limited to a handful of studies (Huxel and Hastings 1999, Vellend 2003, Grainger et al. 2011). Nonetheless, funding for tropical forest restoration is increasingly available from national payment for ecosystem services programs and climate change mitigation initiatives such as Reducing Emissions from Deforestation and Forest Degradation (REDD+, Edwards et al. 2010). These institutions require sub-national prioritization criteria to effectively allocate limited funding and conform to environmental safeguards.

To address this need, we used a unique tropical restoration experiment replicated across a human-dominated landscape ~100 km^2 to evaluate interactions between local restoration, landscape context, and bird community composition and functional groups. As a conservation-relevant measure of composition, we used a similarity index comparing bird communities in restoration sites to those in old-growth forests. We also analyzed three functional groups (frugivores, migrant insectivores, and nectarivores) as predictors of bird-mediated ecosystem functions (seed dispersal, arthropod reduction, and pollination; Table 2.1).

To evaluate local and landscape effects of restoration on birds we: (1) quantified the spatial scale at which bird community composition and functional groups are affected by landscape tree cover; and (2) developed models to predict these attributes using local restoration treatment, landscape tree cover, and their interaction. We analyzed birds because there are well-established correlations between bird community attributes and ecosystem functions (Table 2.1) and because birds respond rapidly to alteration of habitat structure and composition (Reid et al. 2012a).

Table 2.1. Correlates of bird-mediated seed dispersal, arthropod control, and pollination in tropical ecosystems.

Bird community attribute (x)	Ecosystem function (y)	Relationship (R^2)
Frugivore abundance	Dispersed seed richness	$\hat{y} = 0.876x - 5.070$ (0.95)[*]
	Dispersed seed abundance	$\hat{y} = 0.202x - 2.408$ (0.71)[*]
Migrant insectivore richness	% Reduction in total arthropod abundance	$\hat{y} = 10.029x - 40.785$ (0.64)[†]
	% Reduction in large arthropod abundance	$\hat{y} = 8.7336x - 8.3759$ (0.68)[†]
Nectarivore abundance	Quantity and quality of flower pollination	*na*[‡]

[*] Pejchar et al. (2008) *Biol Conserv* **141**, 536–544.

[†] van Bael et al. (2008) *Ecology* **89**, 928–934.

[‡] No study has yet related attributes of avian nectarivore communities to pollination functions. We use nectarivore abundance rather than species richness because vertebrate pollination networks are characterized by low dependency.

Figure 2.1. Local restoration treatments randomly applied to plots of heavily degraded pasture at 13 sites in 2004-2006 in southern Costa Rica. Control plots were cleared of vegetation and allowed to regenerate naturally; islands were cleared and planted with 86 seedlings of four species in six patches (two each 4×4, 8×8, 12×12 m); plantations were cleared and planted in uniform rows throughout the plot (313 seedlings).

2.3. Methods

Birds were quantified through observation over two years (2009-2011) at 13 restoration sites initially established on heavily degraded pasture land in 2004-2006. Each site included three 50 × 50 m plots, which were randomly assigned to one of three treatments. Controls were cleared and abandoned, islands were planted with patches of trees, and plantations were planted with trees across the entire plot (Figure 2.1). Seedlings planted in islands and plantations were a mix of two native timber species, *Terminalia amazonica* (Combretaceae) and *Vochysia gutaemalensis* (Vochysiaceae), and two fast-growing legumes, *Erythrina poeppigiana* and *Inga edulis* (Fabaceae). Sites were cleared with machetes for 2.5 y to allow planted seedlings to grow above existing grasses and forbs. Treatments had been in place for 5-7 y when bird counts took place. Detailed descriptions of restoration treatments are provided elsewhere (Cole et al. 2010).

Birds in restoration sites were surveyed by J.A.R. in Dec 2009 and Apr, Jul, and Nov 2010 and 2011. Each experimental plot at each site was actively searched in a random order for 20 min per observation and all birds seen or heard were recorded. Old-growth forest point count surveys were conducted in May-Sep 2010 at Las Cruces Biological Station Forest Reserve (6 survey points; 8° 47' 7" N, 82° 57' 32" W) and La Amistad Biosphere Reserve (6 survey points near Las Alturas Biological Station, 8° 56' 43" N, 82° 50' 00" W). Four old-growth forest points were interspersed among the restoration sites, and two were 21-28 km from any restoration sites. Each point count was conducted for 30 min by J. Figueroa-Sandí within a maximum radius of 50 m. All surveys were conducted from sunrise (~5:30 AM) until 9:00 AM. Bird taxonomy follows the American Ornithologists' Union Checklist of the Birds of North America and its supplements (American Ornithologists' Union 1998).

To compare community composition of birds in restoration plots and old-growth forests, we used a presence-absence matrix to calculate a Sørensen similarity index: $QS_{ij} = 2C_{ij}/S_i + S_j$, where C is the number of species in common between sites i and j and S is the total number of species at a given site (Oksanen et al. 2012). Migratory songbirds were excluded from the similarity analysis due to different sampling seasons for restoration sites and reference forests. No other seasonal trends were evident. Migrants were included for functional analyses, which did not involve comparisons to old-growth forest. We used a Mantel test of a similarity matrix and distance matrix to evaluate potential for spatial autocorrelation. After removing an outlying reference forest site (La Amistad) that was 21-28 km from all restoration sites, similarity values between sites were not explained by proximity ($r = 0.19$, $p = 0.116$, 9999 permutations).

Avian functional groups (frugivores, migrant insectivores, nectarivores) were assigned based on natural history data (Stiles and Skutch 1989). Because we were interested in guilds as they relate to ecosystem function, seed predators (*i.e.*, Psittacids) and species that eat fruit but rarely defecate viable seeds in the study region were not considered frugivores (Lindell et al. 2012). We selected functional group response variables because they correspond to ecosystem functions that benefit society. Frugivore abundance is a strong predictor of seed rain richness ($r^2 = 0.95$) and abundance ($r^2 = 0.71$)(Pejchar et al. 2008, but see García and Martínez 2012), and migrant insectivore richness was the best community predictor of arthropod reduction in coffee agroforestry in southern Mexico ($r^2 = 0.64$)(Van Bael et al. 2008). We assumed that nectarivore abundance would have greater power than species richness for predicting pollination because vertebrate pollination networks are characterized by low dependency (Bascompte and Jordano 2007), however this hypothesis has not been tested.

Tree cover was classified by manually digitizing aerial photographs from 2003 and 2005 with 2-m resolution (Mendenhall et al. 2011). Tree cover includes primary and secondary forest fragments of all sizes, single trees, early secondary growth, live fences, hedgerows, non-native timber and fruit tree plantations, and nonnative garden ornamentals.

We analyzed bird communities using linear mixed-effects models and maximum likelihood model selection (Burnham and Anderson 1998, Gelman and Hill 2006). First we built two sets of models using local restoration treatment and landscape tree cover. One model set included a landscape × local interaction term and the other did not. Each set included individual models with percent tree cover calculated within 36 concentric rings (10-1000 m radius) around each experimental plot at each site. Responses were modeled using log-link for Poisson-distributed responses and identity-link for normally-distributed responses. For all models we used a random effect term for site. We also used a random term for repeated measures in models that included multiple observations (*i.e.*, frugivore and nectarivore abundance). We used AIC scores and weights corrected for small sample sizes (AIC_c) to select the best model from each set. Then we compared the best model to a model including only local restoration treatment. The model with the lowest AIC_c weight is reported. Effects of local restoration treatments on avian communities were also analyzed using non-parametric Kruskal-Wallis and Wilcoxon rank sum tests. For the frugivore abundance analysis, we excluded one site from the model selection procedure because it had a disproportionate influence for models with small tree cover radii. Significance of individual fixed factors was assessed by removing one factor from the model and comparing AIC_c scores. Model building and comparison analyses were conducted in R 2.15.0 (R Development Core Team 2012) using the lme4 package (Bates et al. 2011).

Overall patterns in community composition should reflect combined trends of individual species. To assess whether patterns observed at the community level made good predictions at the individual species level, we inspected plots of the most abundant species in each group across sites and tree cover gradients.

Our analytical approach addresses several common criticisms of bird community studies in conservation biology. First, forest dependency indices and species richness metrics are problematic (Ruiz-Gutiérrez et al. 2010, Mendenhall et al. 2012). We avoided this issue by using similarity to old-growth forest as a response variable rather than abundance or richness of forest-dependent birds. Second, recent studies have highlighted heterogeneous bird detectability in different habitats, which may confound cross-habitat comparisons (MacKenzie and Royle 2005). Whereas statistical solutions exist, we addressed this problem by intensively surveying small areas, where detection probability was likely ~1. Third, many studies compare birds across small spatial scales and are biased by spatial autocorrelation (Hill and Hamer 2004). Sites in this study were sufficiently spaced (>700 m separation), but plots within sites were separated by only ~10-200 m. This spatial arrangement is appropriate because we were interested in relative habitat usage by birds presented with a choice of three restoration treatments at each site. As such, we use site as a random factor in our modeling procedure. Finally, some authors have criticized the interpretation of studies using small plots because individual patches or restoration treatments are not large enough to support the complete life cycle for a viable population of a given species (Lindell 2008). We do not assume that any birds complete their life cycle within the restoration sites or that interventions have restored bird communities *per se*. Rather, we infer that bird presence denotes that restored habitat supports one or more aspects of a bird's ecology.

2.4. Results

Based upon 3852 detections of 125 species, we found that avian functional guilds and compositional similarity to old-growth forest differed among local restoration treatments (all $X^2 \geq 14$; $p < 0.001$). Plantations were always significantly greater than controls (all $p < 0.01$) and islands were intermediate (Table 2.2).

Models predicting community similarity to old-growth forest, frugivore abundance, and necatrivore abundance were optimized using a term for landscape tree cover at spatial scales of 0.35-0.55 km radius around restoration sites (Figure 2.2, Tables 2.3-2.4). Migrant insectivore richness, however, was only predicted by local restoration treatment (Table 2.5).

For compositional similarity to old-growth forest, landscape effects included an interaction with local restoration treatment (Figure 2.3a). Bird community composition more closely resembled reference forest in experimental plots that were intensively restored in landscapes with higher tree cover (adj. $r^2 = 0.83$, $p < 0.001$; Tables 2.3, 2.4, 2.6).

Frugivore and nectarivore abundance per observation declined as tree cover in the surrounding landscape increased (Figure 2.3b,c), but local × landscape interactions were not significant. Landscape effect was much weaker than local restoration treatment (Table 2.5) and was not reflected in the trends of individual species (Table

2.6). Of the ten most abundant species in each analysis group, eight frugivores, seven nectarivores, nine migratory insectivores, and eight reference forest species had consistently greater abundance in plantation treatments than controls (Table 2.6). Half of the ten most frequently detected old-growth forest species increased in abundance in plantations relative to controls as tree cover increased, as predicted by the best fit model, but no species showed a clear decline in detections as tree cover increased.

Table 2.2. Local restoration effects on avian community attributes. Significant differences ($\alpha = 0.05$) are denoted by ^{AB}.

	Control	Island	Plantation	X^2	*p*
Frugivores (detections/observation)	3.3 ± 0.4^{A}	6.8 ± 0.5^{B}	9.7 ± 0.5^{B}	16.4	<0.001
Nectarivores (detections/observation)	1.4 ± 0.2^{A}	3.0 ± 0.3^{B}	4.4 ± 0.4^{B}	19.0	<0.001
Migrant insectivores (species richness)	1.7 ± 0.4^{A}	4.9 ± 0.6^{B}	6.2 ± 0.5^{B}	19.6	<0.001
Similarity to old-growth (QS)	0.12 ± 0.01^{A}	0.18 ± 0.01^{A}	0.23 ± 0.02^{B}	18.8	<0.001

Table 2.3. Maximum likelihood model selection for bird community attributes. K denotes the number of parameters in the model, and w_i denotes the model weight (i.e., relative likelihood).

Response variable	Model (fixed effects)	K	ΔAIC_c	w_i
Similarity to reference forest	int + treatment	5	2.87	0.24
	int + treatment + tree cover	6	4.88	0.87
	int + treatment × tree cover	8	0.00	1.00
Frugivore abundance	int + treatment	5	3.31	0.19
	int + treatment + tree cover	6	0.00	1.00
	int + treatment × tree cover	8	1.41	0.49
Migrant insectivore richness	int + treatment	5	0.00	1.00
	int + treatment + tree cover	6	2.62	0.27
	int + treatment × tree cover	8	2.15	0.34
Nectarivore abundance	int + treatment	5	2.19	0.34
	int + treatment + tree cover	6	0.00	1.00
	int + treatment × tree cover	8	0.62	0.73

Table 2.4. Maximum likelihood tests for significance of fixed factors explaining bird community attributes

Response variable	Hypothesis	ΔAIC	X^2	*p*
Similarity to reference forest	β(treatment) = 0	-32.0	40.0	<0.001
	β(tree cover) = 0	-5.8	11.8	0.008
	β(interaction) = 0	-7.8	11.8	0.003
Frugivore abundance	β(treatment) = 0	-114.0	118.0	<0.001
	β(tree cover) = 0	-2.7	4.7	0.029
Migrant insectivore richness	β(treatment) = 0	-33.0	37.0	<0.001
Nectarivore abundance	β(treatment) = 0	-78.3	82.3	<0.001
	β(tree cover) = 0	-2.3	4.3	0.039

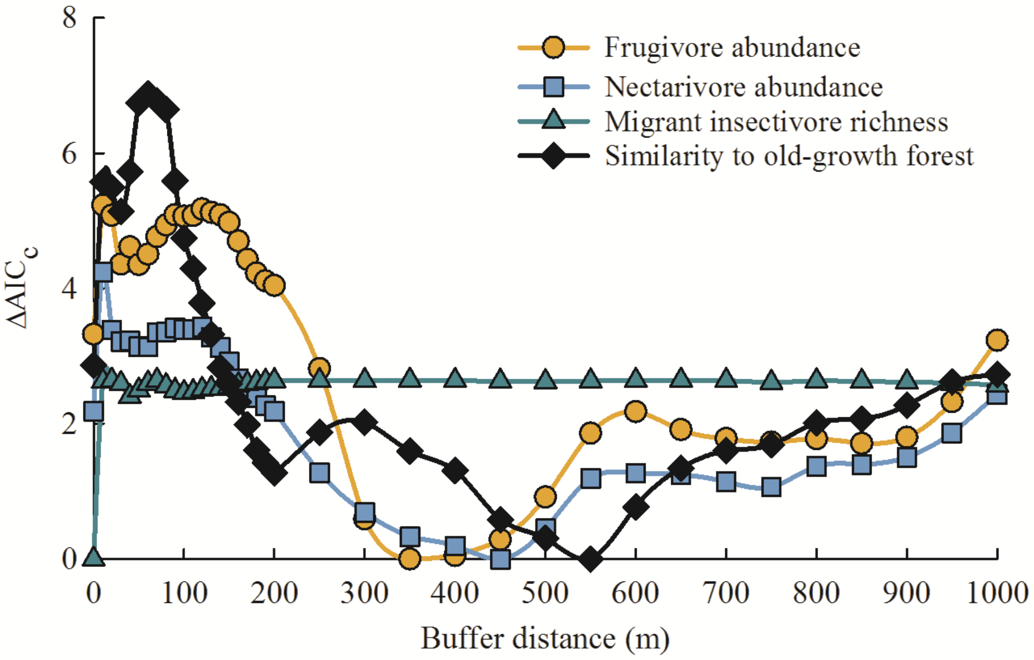

Figure 2.2. Scaling of landscape effects: model fits for community similarity to old-growth forest (diamonds) and functional groups (frugivores = circles; nectarivores = squares; migrant insectivores = triangles) predicted by tree cover at varying buffer distances around restoration sites. AIC_c represents an Akaike Information Criterion score corrected for small sample sizes. ΔAIC_c represents the difference in AIC_c scores between a given model and the model with the lowest AIC_c.

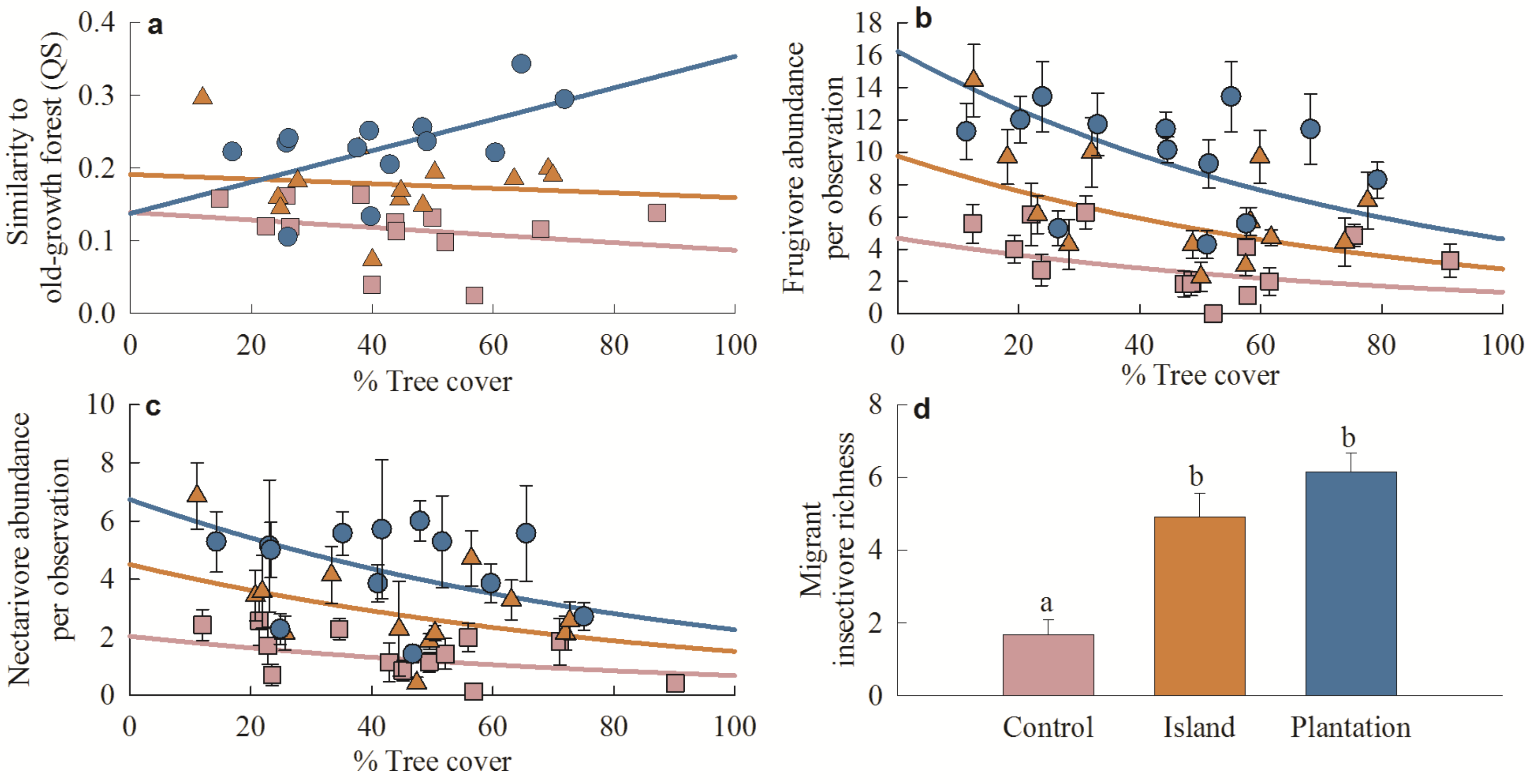

Figure 2.3. Compositional and functional attributes of bird communities predicted by local restoration treatments and landscape-scale tree cover. Error bars represent ± 1 s.e.m. (a-c) Controls are represented by squares; islands by triangles, and plantations by circles. (a) Bray-Curtis similarity of bird communities in restoration sites to bird communities in reference forest (550 m tree cover buffer); (b) frugivore abundance per observation (7 observations per point; 350 m buffer); (c) nectarivore abundance per observation (450 m buffer); (d) migrant insectivore richness (equal sampling intensity). Significance calculated using pairwise Wilcoxon rank sum tests with Bonferroni corrections (all $P < 0.004$).

Table 2.5. Model estimates for bird community attributes in tropical forest restoration.

Response variable	Model fit adj. r^2/P	Parameter	Level	Estimate	s.e.m.
Similarity to old-growth forest	0.83/<0.001	intercept	-	0.139	0.034
		treatment	island	0.052	0.036
			plantation	-0.002	0.037
		tree cover	550 m	-0.052	0.071
		interaction	island × tree cover	0.023	0.077
			plantation × tree cover	0.268	0.081
Frugivore abundance	0.59/<0.001	intercept	-	1.544	0.302
		treatment	island	0.734	0.117
			plantation	1.243	0.111
		tree cover	350 m	-1.255	0.573
Migrant insectivore richness	0.54/<0.001	intercept	-	0.523	0.215
		treatment	island	1.068	0.248
			plantation	1.291	0.241
Nectarivore abundance	0.36/<0.001	intercept	-	0.713	0.263
		treatment	island	0.292	0.131
			plantation	1.195	0.126
		tree cover	450 m	-1.089	0.516

Table 2.6. Individual trends for the ten most abundant bird species in each functional group and the ten most frequently detected species in old-growth forest. Taxonomy follows the American Ornithologists' Union (2007) and its supplements. Species are ordered by group and by the number of detections or by the number of occurrences in reference forest plots.

Group & family	Species	Detections (N)	% Detections in group (%)	Sites with greater observations in plantations than controls / sites where species occurred	Trend in abundance with increasing tree cover
Frugivores					
Thraupidae	*Ramphocelus costaricensis*	273	15.0	7/13	none
Parulidae	*Basileuterus rufifrons*	134	7.4	10/11	none
Incertae Sedis	*Saltator maximus*	124	6.8	8/13	none
Turdidae	*Catharus ustulatus*	120	6.6	11/13	none
Turdidae	*Catharus aurantiirostris*	108	6.0	8/13	none
Thraupidae	*Thraupis episcopus*	96	5.3	6/12	none
Parulidae	*Oreothlypis peregrina*	95	5.2	13/13	none
Incertae Sedis	*Saltator striatipectus*	89	4.9	3/12	none
Tyrannidae	*Zimmerius vilissimus*	75	4.1	7/12	none
Thraupidae	*Tangara larvata*	72	4.0	11/12	none
Nectarivores					
Trochilidae	*Amazilia tzacatl*	211	26.0	12/13	none
Incertae Sedis	*Saltator maximus*	122	15.0	8/13	none
Thraupidae	*Thraupis episcopus*	96	11.8	6/13	none
Parulidae	*Oreothlypis peregrina*	92	11.3	13/13	none
Emberizidae	*Chlorospingus ophthalmicus*	65	8.0	3/4	none
Incertae Sedis	*Coereba flaveola*	46	5.7	7/11	none
Trochilidae	*Phaethornis guy*	39	4.8	9/11	none
Picidae	*Melanerpes rubricapillus*	36	4.4	9/9	slight decrease
Trochilidae	*Amazilia Edward*	30	3.7	3/9	none

Table 2.6. continued

Group & family	Species	Detections (N)	% Detections in group (%)	Sites with greater observations in plantations than controls / sites where species occurred	Trend in abundance with increasing tree cover
Icteridae	*Psarocolius decumanus*	20	2.5	1/3	none
Migrant insectivores					
Turdidae	*Catharus ustulatus*	120	25.2	11/13	none
Parulidae	*Setophaga pensylvanica*	99	20.8	12/12	none
Parulidae	*Oreothlypis peregrina*	92	19.3	13/13	slight decrease
Parulidae	*Geothlypis philadelphia*	67	14.1	7/11	none
Parulidae	*Cardellina pusilla*	29	6.1	7/12	none
Parulidae	*Setophaga fusca*	19	4.0	7/9	none
Icteridae	*Icterus galbula*	13	2.7	5/6	none
Parulidae	*Mniotilta varia*	11	2.3	4/6	none
Parulidae	*Setophaga petechia*	8	1.7	3/5	none
Cardinalidae	*Piranga rubra*	7	1.5	2/5	slight increase

Table 2.6. continued

Group & family	Species	Detections (N)	% Detections in group (%)	Sites with greater observations in plantations than controls / sites where species occurred	Trend in abundance with increasing tree cover
Old-growth forest species					
Formicariidae	*Formicarius analis*	4 (12)	0.2	2/2	increase
Vireonidae	*Hylophilus decurtatus*	7 (12)	0.3	1/4	none
Troglodytidae	*Henicorhina leucosticta*	34 (12)	1.5	5/6	increase
Emberizidae	*Arremon aurantiirostris*	1 (11)	0.0	0/1	none
Emberizidae	*Chlorospingus ophthalmicus*	65 (10)	2.8	3/4	increase
Tyrannidae	*Zimmerius vilissimus*	73 (10)	3.2	7/12	none
Tyrannidae	*Lophotriccus pileatus*	30 (10)	1.3	10/10	increase
Pipridae	*Corapipo altera*	3 (10)	0.1	2/2	increase
Turdidae	*Turdus assimilis*	9 (10)	0.4	4/5	none
Momotidae	*Momotus momota*	15 (9)	0.6	5/9	none

2.5. Discussion

Our results show that local restoration and landscape context interacted to predict bird community composition but not functional groups. Compared to less intensive restoration practices, tree plantations had: (1) greater abundance of frugivores and nectarivores, (2) greater migratory insectivore species richness; and (3) greater compositional similarity to old-growth forest. Old-growth similarity increased with greater amounts of tree cover in the surrounding landscape, but only in plantations. In contrast, frugivore and nectarivore abundance and migrant insectivore richness were greatest in tree plantations regardless of matrix composition. These trends were reflected in the relative abundance of individual species.

Scaling of landscape effects was similar (0.35-0.55 km radius) for old-growth similarity, frugivores, and nectarivores, but the direction of these effects was surprisingly different. Variance in local × landscape interactions for old-growth similarity and functional groups may be best explained by dispersal limitation and niche complementarity. Functional groups are delineated on the basis of species traits, such as diet (Sekercioglu 2006), but species identity is central to measures of community composition and associated conservation value. High similarity values in plantations embedded within well-forested landscapes are contingent upon birds dispersing from pre-existing forest into restoration sites. Strong evidence shows that some forest birds are unable to cross even small distances through unusable habitat (Ibarra-Macias et al. 2011), and that the most dispersal-limited species are typically also the most prone to extinction in fragmented landscapes (Moore et al. 2008). Fragmentation studies have often highlighted that terrestrial insectivores are among the most extinction-prone birds (Stouffer et al. 2009). We report a similar and inverse trend for restoration; the most frequently detected species in old-growth forest was a terrestrial insectivore, *Formicarius analis*, which was only recorded in two restoration sites adjacent to old-growth forest. Intensive local restoration efforts may thus provision suitable habitat for forest-dependent species, but their colonization depends upon matrix permeability and habitat connectivity (Ricketts 2001).

In contrast to old-growth forest birds, frugivores, nectarivores, and migrant insectivores were more abundant or speciose in tree plantations than in less-intensive restoration treatments regardless of landscape context. This observation could result from niche complementarity – the tendency of species similar on one niche axis to differ along another. In our study area, frugivores, nectarivores, and insectivores that are otherwise similar (sometimes congeneric) are separated by habitat affinity into partially overlapping agricultural and forest communities (Mendenhall et al. 2011). The result is a portfolio effect, where reductions in forest-affiliated frugivores, for example, are balanced by increased abundance of agriculture-affiliated frugivores (Karp et al. 2011), potentially maintaining a constant level of bird-mediated ecosystem functions despite high species turnover, though it should be noted that species "replacing" one another may have important behavioral differences that influence function (Rosenfeld 2002). In this context, intensive local restoration in sites with low landscape tree cover may attract agriculture-affiliated birds already present in the surrounding matrix by provisioning food resources, favorable microclimate, or cover from diurnal predators (Fink et al. 2009).

Subtle community-wide increases in frugivore and nectarivore detections in sites with lower tree cover may be explained by the marginal value theorem of optimal foraging (Charnov 1976). If lower tree cover in the surrounding landscape indicates greater travel distances between patches, then birds may spend more time and potentially be detected more frequently exploiting food resources in restoration sites with little tree cover in the surrounding landscape. This observation suggests that smaller forest elements become more valuable (to a subset of the regional bird species pool) when they make up larger proportions of local forest cover. A lack of landscape tree cover effect on migrants compared to other groups could be due to territorial exclusion if individuals are commonly relegated to low quality patches (Marra et al. 1993) or from a general preference for early-successional habitats (Blake and Loiselle 2001). Alternately, hierarchical landscape selection by migrants could occur at a spatial scale larger than the maximum buffer of 1 km used here (Hutto 1985).

Differences in landscape effects on old-growth forest species and functional groups provide novel insights for the relationship between biodiversity and ecosystem functioning and services in ecological restoration. A growing body of literature is establishing connections between biodiversity and ecosystem functioning (BEF) (but see Wardle et al. 1997, Schwartz et al. 2000, Hooper et al. 2005, Naeem et al. 2012), but trade-offs between ecosystem services like carbon sequestration and conservation-relevant biodiversity outcomes are evident for ecological restoration at national and global scales (Mason et al. 2012, Phelps et al. 2012). Terminology is a primary hang-up. *Biodiversity* in the BEF conversation is taken to include taxonomic, phylogenetic, genetic, functional, spatial, temporal, interaction, and landscape diversity (Naeem et al. 2012), but conservation priorities are typically designated using other biodiversity concepts, such as the richness or abundance of threatened, endemic, and forest-affiliated species, population diversity, and community composition (Myers et al. 2000, Roberts et al. 2002, Mendenhall et al. 2012). Our data suggest that this divide between basic and applied biodiversity-ecosystem function science may extend to bird communities if bird-mediated functions are redundant across species or do not align with species-specific conservation priorities.

The local × landscape interaction that we detected for predicting old-growth species composition has important implications for allocating restoration funds at sub-national scales. Large-scale tropical forest restoration is on the rise, due in large part to increased funding from REDD+ and various payments for ecosystem services programs. Our data suggest that new restoration projects in areas with high forest cover will likely promote greater recolonization by species representative of reference communities – and thus safeguard biodiversity conservation – than similar projects in habitat-poor landscapes. Also, more intensive local interventions are likely to benefit birds over a 5-7 yr period more than less intensive or passive restoration techniques. Given time, we expect that effects of local restoration treatments will converge as low-intensity control plots increasingly resemble closed-canopy forest, but landscape effects are likely to endure.

We have demonstrated experimentally that intensive local restoration of degraded pastures promotes three avian functional groups regardless of surrounding tree cover. Also, intensive restoration coupled with high amounts of surrounding tree cover increases habitat for species affiliated with old-growth forest within a few years of the intervention. We note thatlhile ecological restoration holds great hope for slowing or reversing the tide of biodiversity loss (Young 2000), restoration cannot be considered a substitute for the preservation of existing forest (Gibson et al. 2011).

2.6. Acknowledgements

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3. Artificial bat roosts did not accelerate forest regeneration in abandoned pastures in southern Costa Rica

3.1. Summary

Artificial roosts have been proposed as a tool for augmenting bat populations and catalyzing tropical forest regeneration. In the best case scenario, roosts would attract seed-carrying bats (Family Phyllostomidae) into degraded pastures and form nucleating patches of native vegetation. We tested this scenario by monitoring 48 artificial roosts in pastures and adjacent forest fragments in southern Costa Rica over two years. Half of the pasture roosts were exposed to direct sunlight and half were affixed to 4-m living stakes of *Erythrina poeppigiana* (Walp.) O.F. Cook that provided shade. After two years, 94% of roosts in forest and 40% of roosts in pasture had been used by bats at least once – primarily for nocturnal feeding. Maximum daily temperature inside of roosts was the best microclimatic predictor of bat visitation. We identified at least five species of bats that visited roosts, including two frugivores (*Carollia* and *Glossophaga* spp.). Bat-mediated seed dispersal increased with the number of frugivorous bat detections at roosts, but seedling recruitment did not increase with either bat detections or seed abundance over a two-year period. Given that bats rarely used roosts in pastures, and bat visitation did not increase seedling recruitment, our data suggest that artificial bat roosts did not accelerate forest regeneration in abandoned, premontane pastures in southern Costa Rica. This method

could be refined by investigating alternative roost designs, barriers to seedling recruitment below roosts, improvement of roost microclimatic conditions in pastures, and ability of bats to detect roosts in different habitats.

3.2. Introduction

Tropical deforestation exacerbates climate change, undermines rural livelihoods, and disarticulates the most diverse terrestrial communities on the planet (Chhatre and Agrawal 2009; Myers et al. 2000; Pan et al. 2011). Some 27 million hectares of tropical forest were cleared between 2000 and 2005, two-thirds of which were in Latin America (Hansen et al. 2008). The impacts of this forest loss can be partially mitigated through ecological restoration – the process of assisting the recovery of degraded ecosystems to their historic trajectories (SER 2004; Lamb et al. 2005; Rey Benayas et al. 2009). Many degraded lands will regenerate naturally (Chazdon 2003; Letcher and Chazdon 2009), but when succession is arrested or time is of the essence, active intervention may be necessary to overcome barriers to recovery (Holl and Aide 2011; Martínez-Garza and Howe 2003).

Cattle pastures are ubiquitous throughout the tropics and frequently represent an endpoint in the process of land conversion following deforestation. As grazed hillsides become eroded and rural farmers seek opportunities in cities, these lands are often sold or abandoned (Rey Benayas et al. 2007). As such, pastures have become a focus in the literature on tropical forest restoration (Holl and Kappelle 1999). Natural regeneration in pastures is limited by a suite of factors including sparse seed banks and seed rain, high seed predation, and poor germination, survival, and growth (Aide and Cavelier 1994; Cubiña and Aide 2001; Holl 1999; Nepstad et al. 1996). Of these, seed rain is often considered a primary limitation because other barriers to establishment come into play only when seeds are present. Because the majority of Neotropical trees have seeds dispersed by animals (Howe and Smallwood 1982), a challenge for practitioners is to increase animal visitation to areas with reduced habitat resources, stressful microclimate, and increased predation risk.

Standard restoration practice in tropical pastures is to plant trees. Tree planting is an effective strategy because it ameliorates multiple barriers to natural regeneration including seed limitation (Cole et al. 2010; Lindell et al. 2012) and seedling survival and growth (Cole et al. 2011). Establishing tree plantations, however, is expensive and can result in significant legacy effects, such as altered nutrient cycling and tree species composition compared to natural secondary forests (Celentano et al. 2011). As a result, many researchers are now exploring more low-cost, light-handed interventions to catalyze forest regeneration. These have included: bird perches (Aide and Cavelier 1994; Holl 1998a; Miriti 1998; Zanini and Ganade 2005), essential oils of bat-dispersed fruits (Bianconi et al. 2012), giant stakes (Zahawi 2008), artificial bat roosts (Kelm et al. 2008), and applied nucleation (Holl et al. 2011).

Among these novel applications, artificial bat roosts are particularly promising. Neotropical fruit bats (family Phyllostomidae) are among the most important seed dispersers in early successional ecosystems (Fleming 1988; Galindo-González et al. 2000; Muscarella and Fleming 2007; Mello et al. 2008), but deforestation and forest degradation threaten many populations (Fenton et al. 1992; Schultze et al. 2000; Hutson et al. 2001). Bats in deforested landscapes may be limited by shortages of food or suitable roosts, excessive pesticides, or persecution by humans (Mickleburgh et al. 2002; Evelyn and Stiles 2003; RELCOM 2009). Frugivorous Phyllostomids in Costa Rica use a variety of roost types including caves, hollow trees, vine tangles, human infrastructures, and foliage (Foster and Timm 1976; Fleming 1988; Fenton et al. 2000). The premise of the artificial roost strategy is that by provisioning suitable roosts for frugivorous bats, restoration practitioners may attract bats and overcome seed rain barriers in degraded pastures. In the only existing study on this method, researchers installed simulated tree cavities in forest fragments in northern Costa Rica (Kelm et al. 2008). Within a few weeks, up to ten species of bats colonized the roosts in large numbers (up to ~200 individuals per roost). These bats included several frugivores (*Carollia* and *Glossophaga* spp.), and seed rain around the roosts increased significantly compared to seed rain far from the roosts. It is still unknown whether artificial roosts outside of forest fragments will attract bats, or whether increases in seed rain actually translate to increased seedling establishment; a variety of studies demonstrate that seedling recruitment should not be taken for granted (reviewed in Reid and Holl 2012).

The purpose of this experiment was to test whether artificial bat roosts can be used to accelerate forest regeneration in tropical pastures. To do so, we monitored bat activity, seed rain, soil nutrients, and seedling establishment at 48 artificial roosts in abandoned pastures and forests in southern Costa Rica over two years. Our experiment was designed to evaluate (1) whether bats will use artificial roosts in pastures; (2) whether bat activity in roosts increases seed rain and plant-available soil nutrients (N,P); and (3) whether increases in seed rain translate to greater seedling recruitment. We predicted that bats would prefer roosts with greater vegetation cover due to improved microclimate and that bat activity in roosts would increase seed rain and soil nutrients via guano deposition (Duchamp et al. 2010) but not seedling recruitment due to low seed germination and survival in pastures (Holl 1999).

3.3. Methods

3.3.1. Study area

This study was conducted in the countryside surrounding the Las Cruces Biological Station (LCBS; 8° 47′ 7″ N, 82° 57′ 32″ W; rainfall ≈ 4 m y^{-1}; elevation 1100 - 1200 m) in Coto Brus County, Costa Rica. Mean annual temperature is approximately 21°C, and there is a distinct dry season from December to March. The area around LCBS was primarily covered by tropical premontane rainforest (Holdridge et al. 1971) until the 1950s, when government-sponsored immigration led to a population influx and development of the region (Edelman and Seligson 1994). Farm land was primarily used for coffee production until low prices in the 1990s caused many farmers to convert their lands to pasture (Rickert 2005). Currently the landscape is a diverse mix of agricultural fields and forest patches; some 27% of the landscape around Las Cruces Biological Station remained forested in 1994 (Daily et al. 2001).

Soils in our study area vary but are generally characterized by mild acidity, low phosphorus, high organic matter, and aluminum saturation levels below those considered toxic (Holl et al. 2011; Landon 1984; Uehara and Gillman 1981). Pasture vegetation is generally dominated by a mix of native and non-native grasses but also includes many ruderal herbs. The regional bat community includes at least 59 species, of which 23 are primarily frugivorous (LCBS 2012).

3.3.2. Experimental design

We installed 48 artificial roosts at five sites in June-July 2009 (three sites) and July-September 2010 (two sites). In each site, we installed six roosts in degraded pastures and three to six in adjacent forest fragments (based on availability of space). Roosts were randomly assigned to one of three treatments: forest, giant stake, or post (Figure 3.1). Forest roosts were affixed to tree trunks. Pasture roosts were either affixed to wooden or galvanized steel posts exposed to direct sunlight (Post treatment) or to giant stakes of *Erythrina poeppigiana* (Walp.) O.F. Cook (Giant stake treatment; Fabaceae). Giant stakes are large (4 m long) limbs cut from trees that are planted bare and resprout quickly (Zahawi 2008). We used giant stakes to assess whether increased canopy cover from resprouting branches would ameliorate temperature extremes and increase bat visitation to roosts. We planted stakes 50 cm deep and allowed them to grow for three months before affixing roosts. Stakes that died within the first year were replaced. Within a year, most giant stakes sprouted a canopy with a mean area of 2.7 ± 1.7 m^2 (SE).

Each roost was paired with a control plot that did not have a roost. Controls were situated 10 m away from roosts in a random compass direction. At each roost and control, we measured seed rain, soil nutrients, and seedling recruitment. Spacing between roosts and controls reflects spatial constraints imposed by working at multiple study sites on small, private land holdings, and was adequate given observed differences in seed rain between occupied roosts and their paired controls.

3.3.3. Artificial roosts

Roosts consisted of emulated tree hollows constructed using a wooden frame, Fibrolit walls, and a 1.9-cm plastic screen on the ceiling (Figure 3.1). Interior dimensions were 40 × 40 × 60 cm. Fibrolit is an inexpensive construction material made from wood fiber and concrete that is that is widely available in Latin America and is

Figure 3.1. Artificial bat roosts and experimental treatments. (a) post treatment: bat roost affixed to a wooden post in a pasture; (b) giant stake treatment: roost affixed to a giant stake of *E. poeppigiana*; (c) giant stake after two years of growth with a canopy diameter >4 m; (d) forest treatment: roost affixed to a tree with an infrared video camera near the opening. Photos a, b, and d by J.L.R. Photo c by C. Ericson.

Table 3.1. Interior temperatures of artificial roosts (± SE) measured over a two-week period in July 2011.

Treatment	Minimum daily temperature (°C)	Mean daily temperature (°C)	Maximum daily temperature (°C)
Forest	17.6 ± 0.0	19.7 ± 0.1	22.5 ± 0.3
Giant stake	17.1 ± 0.0	20.6 ± 0.1	26.6 ± 0.4
Post	17.2 ± 0.1	20.4 ± 0.2	25.5 ± 0.5

resistant to insects and water. Roosts were open on the bottom to provide access for bats. Roost interiors were dark, and temperatures varied by treatment (Table 3.1). We mounted the roosts on trees or poles 2-3 m above the ground in order for the entrance to be accessible above the level of exotic pasture grasses.

3.3.4. Roost monitoring

Roosts were monitored for bat activity twice per month over a period of two years. Seed traps (see *Seed rain*) below roosts were checked for evidence of bat use (*i.e.*, feces, insect parts, or masticated fruit), and roosts were inspected for colonization (*i.e.*, day-roosting bats). We used motion-activated infrared video cameras and digital photographs to confirm visitation from seed trap evidence and to evaluate bat composition. Cameras were constructed and deployed following Frick *et al.* (2009). We identified bats with Reid (2009) and an unpublished field key for Costa Rica (Timm, York, Rodríguez-H., and Laval).

Microclimate is an important determinant of roost selection by Microchiropteran bats (Boyles 2007). To evaluate the relationship between roost microclimate and bat visitation, we measured roost temperature at 15 min intervals in 25 roosts at three sites over a two-week period in July 2011 (HOBO Pendant® temperature logger, Onset Corporation, Cape Cod, MA). Data loggers were placed inside of the roosts near the ceiling to evaluate as closely as possible the microclimate experienced by roosting bats.

3.3.5. Seed rain

To assess the influence of bat visitation on seed rain, we collected seeds twice per month from each roost and paired control plot. Seed traps were made from fine gauge (0.5 × 0.5 mm) mosquito netting hung from a wire hoop (0.25 m^2) on 50 cm wooden legs. The elevated seed trap design prevented seed deposition by terrestrial animals. A local reference collection was used to identify seeds (Cole et al. 2010). Only seeds that were likely to have been dispersed by bats were included in the analysis. Probable bat-dispersed seeds were identified from a local database of >500 bat fecal samples (D. S. Karp *et al.* unpublished data) and an online database of bat/plant interactions (Geiselman et al. 2002). This method of inference conservatively predicts which seeds may have been dispersed by bats.

3.3.6. Soil nutrients

To assess the influence of bat guano deposition on soil nutrients (N,P), we collected three soil cores (10 cm depth, 2 cm diameter) below each roost and adjacent control at the outset of the study. We conducted follow-up sampling after the first and second years at one site with particularly high bat visitation. Cores were composited and homogenized to represent one sample per roost or control. Plant available nitrogen (N) was extracted with potassium chloride and analyzed colorimetrically with an ammonium salicylate and ammonium cyanurate colorimetric method to detect ammonium (Sinsabaugh et al. 2000) and vanadium (III), and sulfanilamide and N-(1-naphthyl)-ethylenediamine dihydrochloride (NED) to quantify nitrate (Doane and

Horwath 2003). Sum of inorganic N pools was calculated by summing nitrate and ammonium levels of each composited soil sample. Total N was measured by the dry combustion method with an Elemental Combustion CHNS-O analyzer (ECS 4010, Costech Analytical Technologies, Valencia, CA). Phosphorus (P) was extracted with a Mehlich III solution (Mehlich 1984) and analyzed with an Optima 2100DV ICP Optical Emission Spectrometer (Perkin-Elmer, Shelton, CT) for total extractable P and colorimetrically with a continuous flow auto-analyzer (OI Analytical, College Station, TX) for plant-available P.

3.3.7. Seedling recruitment

To assess the overall effect of bat visitation on secondary succession, we measured tree seedling recruitment in a 2-m radius around roosts and controls. During each rainy season (June-September), we counted all seedlings <1 m tall. Initial surveys were conducted within three months of roost installation. Seedlings were identified by a local expert (F. O. Brenes) and from a regional reference collection (http://www.ots.ac.cr/herbarium). Only seedlings likely to have been dispersed by bats were included in the analysis (See *3.3.5. Seed rain*). We also estimated the percent cover of non-grass vegetation in each seedling plot with a ranking system: 0-5, 6-10, 11-25, 26-50, 51-75, 76-95, and 96-100%.

3.3.8. Data analysis

We used linear mixed-effects regression to evaluate the influence of treatments (forest, giant stake, post) on bat visitation. We chose a mixed-effect model because it allowed us to account for the non-Gaussian distribution of bat detections by specifying a Poisson family and log-link function. This framework also allowed us to include a random site effect. We produced separate models for frugivores, insectivores, and all bats combined. The model structure was $y = \beta_0 + \beta_1 x_1 + s_i + \varepsilon_i$ where y is the number of bat detections, β_0 is the y-intercept, β_1 is a vector of fixed-effect coefficients for each of the three treatments (x_1), s_i is the random effect for the ith site, and ε_i is the error term. For pairwise comparisons between treatments, we used a post-hoc test (Tukey's Honestly Significant Difference).

We also performed a survival analysis to assess differences in the time until first roost visit by bats in each treatment. We used a Kaplan-Meier estimator of survival probability (Therneau 2012) and log-rank tests to evaluate differences among treatments in use or colonization probability. We defined *use* as bat visitation to a roost (*i.e.*, for nocturnal feeding) and *colonization* as bats sleeping in a roost during the day.

We used maximum likelihood model selection to evaluate the relationship between roost temperature and bat visitation (Burnham and Anderson 1998). First, we built three linear mixed-effects models with different temperature calculations (daily mean, minimum, and maximum) as fixed factors to explain the number of bat detections over two years. We used a Poisson distribution, log-link function, and a random term for site. Then we calculated Akaike Information Criterion scores corrected for small sample sizes (AIC_c) and selected the best model based on the minimum AIC_c. We also compared models using microclimatic predictors to models using treatment and models using both microclimate and treatment.

We used a Wilcoxon paired sample test to compare differences in soil nutrients between roost and control plots within and across years.

To evaluate the relationship between frugivorous bat detections and seed rain abundance, we used linear mixed-effects regression. We defined a response variable (Δ seed abundance$_i$) as the difference in abundance of bat-dispersed seeds between the *i*th roost and the *i*th control over two years. Positive values represented an increase in seed rain compared to the control, and negative values represented a decrease. The response variable was strongly skewed by several high values but could not be log-normalized or modeled as a Poisson distribution because the data included negative numbers. Instead, we used a rank transformation to normalize the response variable.

We used a maximum likelihood hypothesis-testing approach to evaluate whether bat visitation and seed abundance influenced seedling recruitment. As response variables, we used the difference in the change in tree seedling abundance (Δ tree seedling) and non-grass vegetation cover (Δ non-grass vegetation) between roosts and controls over two years, calculated as $y = (r_2 - r_0) - (c_2 - c_0)$ where y is the response variable (Δ tree seedling or Δ non-grass vegetation), and r_2, r_0, c_2, and c_0 are the measured seedling abundance or non-grass vegetation cover for roosts (r) and controls (c) in years 0 and 2. Values greater than zero denote an increase below roost boxes relative to adjacent controls. For each variable, we constructed three models with the structure $y = \beta_0 + \beta_1 x_1 + \beta_2 x_2 + \mathrm{s}i + \varepsilon_i$ where β_1 is a vector of fixed effect coefficients for each of the three treatments (x_1), and β_2 is a fixed effect coefficient for seed abundance (model 1), ranked seed abundance (model 2), or frugivore detections (model 3). For each model, we used a Gaussian distribution and identity-link function. We evaluated the significance of each fixed factor by removing it from the model and comparing the simpler model to the more complex model based on AIC scores.

Model fit for each of the linear mixed effects regressions was assessed by inspecting plots of residuals and by regressing fitted values against observed values. We used the lme4 package (Bates et al. 2011) in R 2.15.0 (R Development Core Team 2012) for these analyses.

3.4. Results

3.4.1. Use and colonization

During two years of monitoring we detected bat visitations in 26 out of 48 artificial roosts (54%). Seventeen out of 18 forest roosts (94%) were used at least once compared to 12 out of 30 roosts (40%) in pasture. Bats colonized at least three roosts as day roosts, and the remainder was either used as nocturnal feeding roosts or as day roosts for short periods of time (≤ 2 wk). All three day roosts were in forests. At least five bat species used artificial roosts (Table 3.2; Figure 3.2; Supplementary videos 3.1-3.2), three of which colonized roosts permanently, and two of which only used roosts for nocturnal feeding.

Bats used roosts in forest sooner and with greater frequency than roosts in pasture (Figure 3.3a-b). We found a strong treatment effect on bat visitation that was primarily driven by the difference between bat detections in forest versus pasture roosts (Table 3.3). Total bat detections and insectivore detections were greater in roosts affixed to giant stakes than in roosts affixed to posts, but frugivore detections were not statistically different between the two pasture treatments (Table 3.4). Additionally, time until first visitation was shorter in forest than in pasture ($X^2 = 28.4$, $P < 0.001$), but giant stakes and posts did not differ ($X^2 = 2.2$, $P = 0.142$).

Of three microclimatic predictors tested, maximum daily temperature was the best predictor of bat detection probability (Table 3.5). The number of roost visitations in both pasture and forest increased as maximum daily temperature in the roosts decreased, and the majority of bat detections (90.1%) were from roosts with maximum daily temperatures <24°C (Fig. 3.3c). A model using only maximum daily temperature to explain bat visits to 25 roosts over two years was better than models using treatment alone ($\Delta AIC_c = 7.0$) or treatment and maximum daily temperature ($\Delta AIC_c = 26.7$; Table 3.6).

3.4.2. Seed rain

Out of 76 563 seeds collected, 54 763 (71.5%) were from bat-dispersed species. Among bat-dispersed seeds, 84% were from shrubs, 16% were from trees, and less than 1% were from herbs, vines, and lianas. Most seeds were from early-successional genera (94%), particularly *Piper* (78%), *Cecropia* (6%), and *Solanum* (6%), but *Clusia* (a genus that includes many mid-late successional trees) seeds were also common (6%). Seed rain abundance increased exponentially with greater frugivore detections (Figure 3.4). Ranked Δ seed rain abundance increased with the number of frugivore detections for shrub seeds (Adj. $R^2 = 0.30$), tree seeds (Adj. $R^2 = 0.22$), and all seeds combined (Adj. $R^2 = 0.38$, all $P < 0.001$; Table 3.7).

3.4.3. Soil nutrients

Nutrient concentrations did not differ significantly between roosts and adjacent controls over two years (Figure 3.5). Both roosts and controls trended towards a decrease in nutrient levels over two years (all $P = 0.0625$) including total extractable P, total N, and the sum of inorganic N, indicating that variation across years was greater than between roosts and controls.

3.4.4. Seedling recruitment

We recorded 740 tree seedling detections. Sixty nine percent of detections were mid-late successional species, 24% were early successional species, and 6% were non-native agricultural species. *Inga* was the most common genus of bat-dispersed seedling comprising 21% of detections, followed by *Allophylus* (17%), *Miconia* (14%), and *Calophyllum* (13%). Ninety two percent of seedling detections were in forest, and 8% were in pasture (Giant stake = 3%; Post = 5%). Neither tree seedling abundance nor cover of non-grass vegetation (*i.e.*, forbs and shrubs) increased with seed abundance, ranked seed abundance, or frugivore detections (Fig. 3.4b, Table 3.8).

Figure 3.2. *Glossophaga* and *Carollia* bats resting in an artificial roost in forest habitat during the day. Photograph by J.L.R.

Table 3.2. Species composition of bats that used artificial roosts in forests and pastures.

		Number of roosts used[a] (colonized[b])		Max
Species	Diet	Forest	Pasture	individuals
Carollia spp	fruit	1 (1)	1 (0)	2
Desmodus rotundus	blood	2 (0)	0 (0)	--
Glossophaga spp	nectar,fruit	1 (1)	2 (0)	5
Micronycteris spp	insects	2 (1)	0 (0)	6
Mimon crenulatum	insects	1 (0)	0 (0)	2
unidentified spp		15 (3)	16 (0)	8

[a] Use refers to evidence of bat visitation (e.g., feces or masticated fruit in a seed trap).

[b] Colonization refers to observations of bats sleeping inside of roosts during the day.

Table 3.3. Diagnostic statistics for linear mixed-effects models of bat visitation to artificial roosts.

Response (num. detections)	Model fit (Adj. r^2/p)	Parameter	Level	Estimate	SE	P
All bats	0.58/<0.001	intercept	-	2.33	0.28	<0.001
		treatment	giant stake	-1.60	0.17	<0.001
			post	-2.94	0.32	<0.001
Frugivores	0.38/<0.001	intercept	-	0.80	0.47	0.0862
		treatment	giant stake	-1.69	0.36	<0.001
			post	-1.94	0.40	<0.001
Insectivores	0.35/<0.001	intercept	-	-0.05	1.26	0.971
		treatment	giant stake	-1.53	0.28	<0.001
			post	-4.24	1.01	<0.001

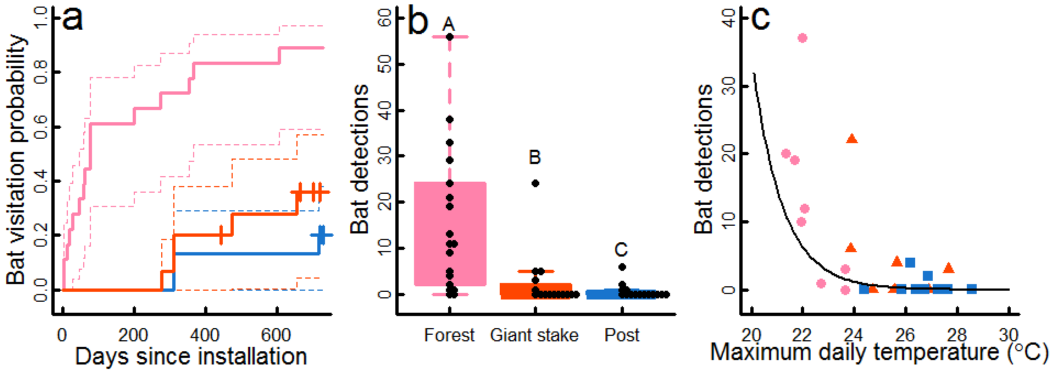

Figure 3.3. Bat detections in artificial roosts during two years of monitoring in forest and pastures in southern Costa Rica. (a) Probability that a roost has been used (*i.e.*, for nocturnal foraging) at least once over time. Treatments are denoted by shading: pink = forest, orange = giant stake; blue = post. Dotted lines represent 95% confidence intervals of Kaplan Meier survival probability. Cross hatches denote roosts that were not monitored for the entire two-year period. (b) Total bat detections in each treatment. Each dot represents one artificial roost. Points are stacked to prevent overplotting. Shaded boxes represent standard box plots. Letters denote statistically significant differences (α = 0.95) from post-hoc tests (Tukey's Honestly Significant Difference). (c) Bat detections as a function of maximum daily temperature inside roosts. Treatment is indicated by shape: circle = forest; triangle = giant stake; square = post.

Table 3.4. Pairwise comparisons of bat visitation to artificial roosts (Tukey's Honestly Significant Difference) in southern Costa Rica.

Response (num. detections)	Hypothesis	Estimate ± SE	*z*	*P*
All bats	$M_{stake}-M_{forest} = 0$	-1.60 ± 0.17	-9.20	*<0.001*
	$M_{post}-M_{forest} = 0$	-2.94 ± 0.32	-9.11	*<0.001*
	$M_{post}-M_{stake} = 0$	-1.34 ± 0.36	-3.76	*<0.001*
Frugivores	$M_{stake}-M_{forest} = 0$	-1.69 ± 0.36	-4.74	*<0.001*
	$M_{post}-M_{forest} = 0$	-1.94 ± 0.40	-4.87	*<0.001*
	$M_{post}-M_{stake} = 0$	-0.25 ± 0.50	-0.50	0.868
Insectivores	$M_{stake}-M_{forest} = 0$	-1.53 ± 0.28	-5.47	*<0.001*
	$M_{post}-M_{forest} = 0$	-4.24 ± 1.01	-4.21	*<0.001*
	$M_{post}-M_{stake} = 0$	-2.71 ± 1.03	-2.62	*0.020*

Table 3.5. Maximum likelihood model selection for the relationship between roost temperature and the number of bat detections over two years.

Fixed factors	AIC_c	ΔAIC_c
Intercept only	235.4	123.5
Intercept + β(mean daily temp)	121.5	9.6
Intercept + β(maximum daily temp)	111.9	0.0
Intercept + β(minimum daily temp)	202.4	90.5

Table 3.6. AIC model comparison for bat roost treatment and maximum daily temperature explaining the number of bat detections over two years.

Fixed factors	AIC_c	ΔAIC_c
Intercept + B(maximum daily temp)	111.9	0.0
Intercept + B(treatment)	118.9	7.0
Intercept + B(maximum daily temp) + B(treatment)	138.6	26.7

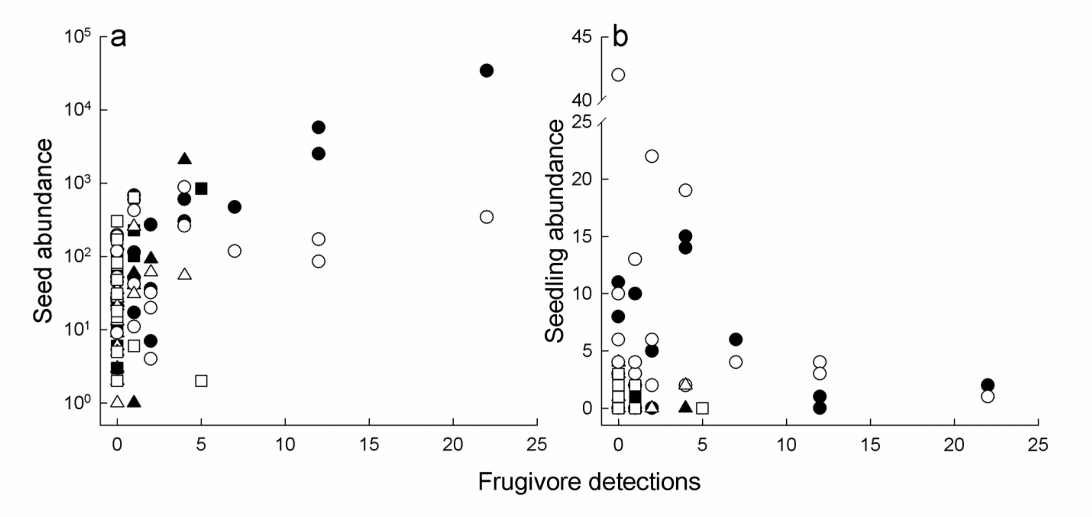

Figure 3.4. Relationship between the number of frugivore detections and seed (a) and seedling abundance (b). Filled shapes represent artificial roosts, and hollow shapes represent controls. Treatment is indicated by shape: circle = forest; triangle = giant stake; square = post. Seed rain abundance is summed over the entire two-year study period. Seedling abundance is from the second year of the experiment.

Table 3.7. Diagnostic statistics from linear mixed effects regression of seed rain attributes.

Seed rain response*	Model fit (Adj. R^2/P)	Parameter	Estimate
all seeds	0.38/<0.001	intercept	-0.26 ± 0.16
		frugivore detections	0.14 ± 0.03
shrub seeds	0.30/<0.001	intercept	-0.25 ± 0.13
		frugivore detections	0.14 ± 0.03
tree seeds	0.22/<0.001	intercept	-0.19 ± 0.15
		frugivore detections	0.16 ± 0.11
Piper spp.	0.31/<0.001	intercept	-0.25 ± 0.13
		frugivore detections	0.14 ± 0.03
Clusia spp.	0.24/<0.001	intercept	-0.07 ± 0.12
		frugivore detections	0.09 ± 0.10
Cecropia spp.	0.22/<0.001	intercept	-0.09 ± 0.25
		frugivore detections	0.09 ± 0.12
Solanum spp.	0.29/<0.001	intercept	-0.24 ± 0.13
		frugivore detections	0.14 ± 0.03

* Seed rain responses represent the rank-transformed difference in seed rain abundance between paired roosts and controls (ranked Δ seed rain abundance).

Table 3.8. Maximum likelihood hypothesis tests for significance of fixed factors explaining differences in the change in tree seedling abundance (Δ seedling abundance) and non-grass vegetation cover (Δ non-grass vegetation) between roosts and controls.

Model	Hypothesis	ΔAIC	X^2	*P*
Δ seedling abundance	β(seed abun.) = 0	7.66	2.3	0.801
	β(rank seed abun.) = 0	8.80	1.2	0.945
	β(frugivore visits) = 0	8.98	1.0	0.961
Δ non-grass vegetation	β(seed abun.) = 0	4.83	5.2	0.395
	β(rank seed abun.) = 0	9.89	0.1	1.000
	β(frugivore visits) = 0	6.37	3.6	0.604

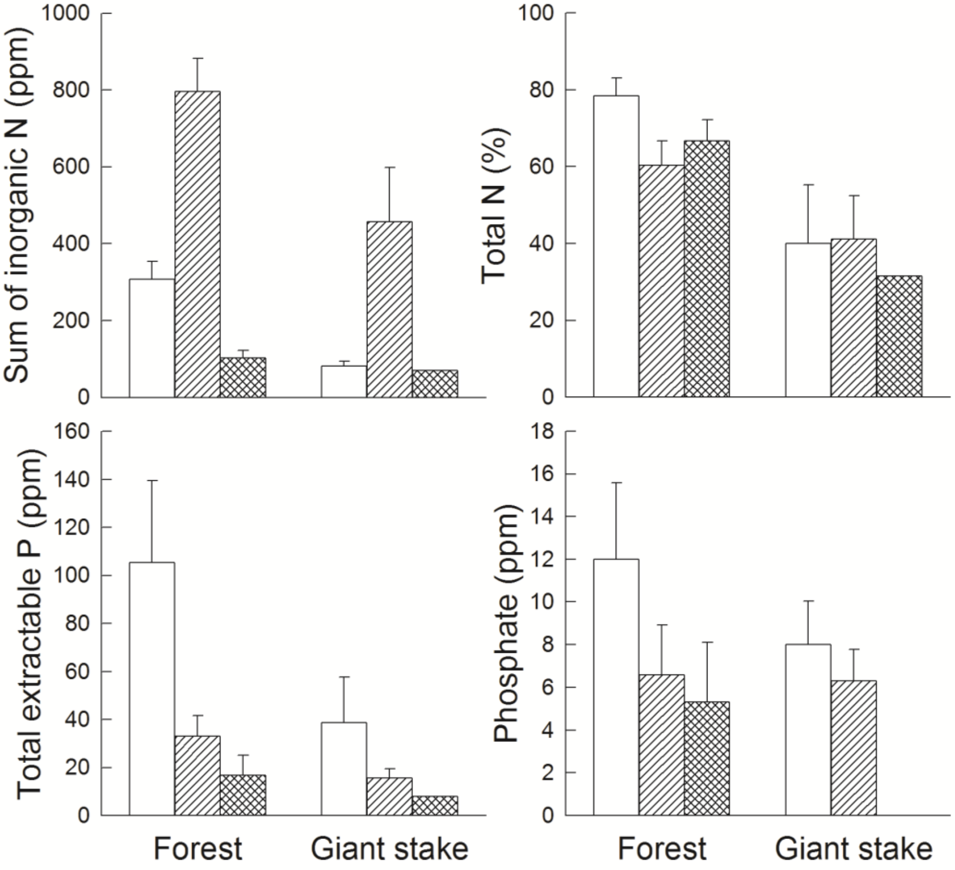

Figure 3.5. Soil nutrient concentrations below artificial roosts at a site with particularly high bat visitation. Error bars represent 1 SE. Sample sizes for forest/giant stakes: 2009 (6/3); 2010 (5/3); 2011 (4/1). Year is denoted by pattern: 2009 = hollow; 2010 = diagonal bars; 2011 = cross-hatch.

3.5. Discussion

For artificial roosts to initiate nucleating succession in tropical pastures: (1) bats must use roosts in pasture; (2) bat visitation must increase seed rain; and (3) increased seed rain must translate to higher seedling recruitment. Our results corroborate previous observations that bats will find and use roosts quickly when they are located in forests and that bat visitation increases seed rain abundance (Kelm et al. 2008). However, bats in our study rarely visited roosts in pastures, and greater seed rain abundance did not lead to higher seedling recruitment over a two-year period. As such, we conclude that artificial roosts did not accelerate forest succession in abandoned pastures in premontane southern Costa Rica.

3.5.1. Why didn't bats visit roosts in degraded pasture?

There are at least three possible explanations for limited bat usage of roosts in degraded pasture. First, roost microclimate may have been unsuitable in pastures (Fig. 2c). Microclimate is an important determinant of roost use in bats (Boyles 2007). Phyllostomid bats in Mexico, for example, preferentially roost in caves with temperature <20° C (Avila-Flores and Medellín 2004). We observed that the most frequently-visited roosts were also the coolest roosts (max. daily temp. < 24° C), both in pasture and in forest. Moreover, a model using only maximum daily roost temperature was a better predictor of bat detections than models using treatment or treatment and maximum daily roost temperature combined. This observation strongly suggests that microclimate is a driver of variance in artificial roost visitation, though further measurements of seasonal variation in roost temperature would be useful.

Roosts may also have been difficult for bats to locate given that there are few resources (*i.e.*, food, shelter) that would cause bats to spend significant amounts of time in degraded pastures. The sensory mechanisms for how bats locate suitable, uninhabited roosts are not well-understood. Noctule bats (*Nyctalus noctula*) and disc-winged bats (*Thyroptera tricolor*) use conspecific echolocation calls to locate suitable roosts (Ruczynski et al. 2007; Chaverri et al. 2013). This habit is not known in the Phyllostomidae, but two large Phyllostomid frugivores, *Artibeus jamaicensis* and *A. lituratus*, appear to use auditory communication in defense against predators (August 1979; Ryan et al. 1985). If Phyllostomid bats also use conspecific signals to find roosts, then time until roost detection could potentially be reduced by playing bat vocalizations from speakers. Similar strategies have worked well for other taxa, such as common murres (*Uria aalge*; Parker et al. 2007). Another technique for improving roost detection could involve olfactory attractants, such as odiferous fruit oils (Bianconi et al. 2012). Both of these concepts warrant further research.

Roosts in this study were modified for use in pastures from the design used by Kelm *et al*. (2008) in northern Costa Rica, and these modifications likely influenced how bats interacted with the roosts. Specifically, our roosts were smaller (96 000 cm^3 vs. $\geq$565 704 cm^3) and the opening had a different orientation that may have allowed in more light (open on the bottom vs. the side). Whereas several bat species in Kelm's study tended to sleep in roosts during the day, bats in our study generally used roosts for nocturnal feeding. Microchiropteran bats in several families preferentially select dark day roosts (Ferrara and Leberg 2005; Usman 1988). If our roosts were brighter than Kelm's, this could explain the observed difference in behavior. Colonized roosts in Kelm's study also had greater absolute numbers of day roosting bats, which could be explained by the greater size of the roosts in that study.

3.5.2. Why didn't increases in seed rain translate to increased seedling recruitment?

The lack of relationship that we observed between seed rain and seedling recruitment in pastures suggests that secondary succession is limited by more than just seed dispersal. Seeds that arrive in degraded pastures have an extremely low probability of survival; as few as 0.1% of seeds in an experiment in montane Costa Rica survived over an 18-mo period (Holl 2002). Seed mortality is attributable to predation, desiccation, and rot (Cole 2009), and the few seedlings that establish are impeded by competition with pasture grasses (Holl et al. 2000) and sometimes intense herbivory (Nepstad et al. 1990). Therefore, restoration applications designed to increase forest regeneration must monitor not only seed dispersal but also seedling recruitment (Reid and Holl 2012). Future studies could isolate the mechanisms that prevent seedling establishment below roosts by comparing the fate of seeds exposed to different groups of predators (Cole 2009), manipulating above- and below-ground competition with ruderal vegetation (Holl 1998b), or reducing nutrient stress by adding fertilizer (Carpenter et al. 2004).

Additionally, seeds dispersed below roosts in forest were likely maladapted for understory abiotic conditions. Most of the seeds recovered in this study were small, light-demanding seeds from early-successional trees and shrubs such as *Cecropia*, *Piper*, and *Solanum*. These observations substantiate isotopic evidence from northern Costa Rica that *Carollia* spp. bats more frequently disperse early-successional seeds to late-successional environments than vice-versa (Voigt et al. 2012). If this is the case, then *Carollia*-dominated bat roosts are also unlikely to meaningfully contribute to seed diversification in secondary forests and tree plantations. Instead, future research should explore the influence of bat roosts in forest on adjacent pasture development, or alternative roost designs to attract a different frugivore assemblage. Planting broad-leaved palms and *Heliconia* spp., for example, could provide roosting habitat for tent-making bats, some of which are known to disperse large, late-successional tree seeds (Melo et al. 2009).

The duration of this study (two years) may have been insufficient for detecting an influence of increased seed rain on seedling recruitment. Seedling recruitment in tropical forests has considerable interannual variability, with large cohorts becoming established in some years, and few individuals establishing in others (Connell and Green 2000; Curran and Webb 2000; Norden et al. 2007). During the years of this study (2009-2012), seedling recruitment in other restoration sites in our study area that have been monitored continuously for six years were not abnormally low (Zahawi et al. 2012), which suggests that interannual variability in establishment was probably not an important factor. Nonetheless, we do not expect that a longer monitoring period would have revealed greater seedling recruitment below bat roosts in our pastures because: (1) seed rain below roosts in pastures was low due to a lack of bat visitation in that habitat, and (2) previous studies suggest that a very large input of seeds would be required to increase recruitment in pastures given extremely low survivorship (Holl 2002).

3.5.3. What effect might insectivorous bats have on forest regeneration?

Our results and the results of a previous study show that in addition to frugivores, leaf-gleaning insectivorous Phyllostomids frequently use artificial roosts (Kelm et al. 2008). We observed that insectivore detections were greater in roosts affixed to giant stakes than in roosts with no shade in open pastures. Exclosure experiments in the Neotropics have shown that insectivorous Phyllostomids reduce arthropod abundance in agroforestry systems (Williams-Guillén et al. 2008) and reduce arthropods and herbivory on seedlings in tropical forests (Kalka et al. 2008). If insectivorous Phyllostomids colonize roosts in regenerating forests or tree plantations, they could improve seedling survival and growth by suppressing invertebrate herbivores.

3.5.4. Conclusions

We have demonstrated experimentally that artificial bat roosts in southern Costa Rica did not accelerate forest regeneration in former pastures over a two-year period because bats rarely used roosts in pastures and increased seed rain below roosts did not translate to greater seedling recruitment. The general approach of manipulating bat behavior to catalyze succession, however, merits further study. Potential areas for future research include alternative roost designs that take into account the gamut of Phyllostomid roosting habits; barriers to seedling establishment below roosts; effects of leaf-gleaning insectivores on herbivore suppression; improvement of microclimatic conditions in roosts in pasture environments; and the ability of bats to detect roosts in different habitats.

3.6. Acknowledgements

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further involvement in the research. Protocols for animal research were approved by an Institutional Animal Care and Use Committee at the University of California Santa Cruz. The authors declare no conflicts of interest.

4. Conservation psychology of bat killing in southern Costa Rica

4.1. Summary

Effective conservation action requires an understanding of the reciprocal relationships between humans and nature. The nascent field of conservation psychology provides a framework and a range of methodologies to fill this critical gap. In this study I used qualitative and quantitative social science methods to investigate the relationship between people and bats - a taxon characterized by frequent appearance in myth and superstition. I found that people in a rural, agricultural county in southern Costa Rica had predominantly negative perceptions about bats and limited knowledge of their natural history. Whereas many farmers likely benefitted from bat-mediated ecosystem services, such as pest control on coffee farms, most reported only negative interactions with bats, such as depredation of livestock by the common vampire bat (*Desmodus rotundus*). Out of 500 male survey respondents, 14% indicated that they had killed roosting bats within the past five years, and 27% said that they if they found a bat roost on their farm they would kill the bats or burn the roost. Using an analysis based on the theory of reasoned action, I found that outcome attitude was more important than normative pressure or perceived control for predicting respondents' intent to kill bats. I identified three beliefs that contributed to outcome attitude: those who were more likely to kill bats thought that it reduced damage and disease transmission to livestock, whereas those were less likely believed that killing

bats reduces ecosystem services and damages nature. The two most important predictors of these beliefs were how much a respondent knew about bat natural history and whether or not he had suffered livestock damage from vampire bats. These results support the idea that environmental education about basic bat biology is efficacious for changing bat killing behavior and reinforcing pro-conservation beliefs. Education alone, however, is probably insufficient; the importance of exposure to damage incurred by vampire bats suggests that conservationists should also focus on on-the-ground support for farmers to safely mitigate bat-mediated livelihood risks.

4.2. Introduction

Human behaviors, whether ecologically destructive or beneficial, are driven by perceptions, beliefs, and decision making; this simple fact speaks to the potential contribution of the nascent field of conservation psychology (Clayton and Brook 2005, Saunders et al. 2006). The premise of conservation psychology is that human-environment relationships are inherently bidirectional and should be treated as such. Its root disciplines, environmental psychology and conservation biology, have demonstrated that nature impacts people and that people have had tremendous reciprocal effects on nature (Meine 2010, Steg et al. 2013). Conservation psychology approaches environmental questions by applying key psychological principles, such as that future behavior is influenced by the consequences of past behavior, and that behaviors have multiple causes that are not sometimes non-rational (Clayton and

Brook 2005). Environmental questions that conservation psychology seeks to answer include (but are not limited to): How do humans learn about, care for, and behave towards nature? (Mascia 2003).

Conservation psychology may be particularly well-suited for exploring the relationship between humans and bats - a taxon that has important impacts on society and frequently appears in myth and superstition (Hill and Smith 1984). For many people, bats evoke fear and disgust (Knight 2008) - emotional responses that were captured in and reinforced by Bram Stoker's (1897) *Dracula* and many books and films since. However, bats may also be revered. In China, bats are traditionally recognized as symbols of happiness and good fortune (Kunz 1984). Bats have also figured prominently in some indigenous religions in Mesoamerica and South America (Hill and Smith 1984); a vampire bat is a central character in the creation myth of the Bribri of Costa Rica, for example (Rodríguez-Herrera 2012).

Kunz et al. (2011) reviewed the tangible benefits that bats provide to humanity. These benefits include arthropod control (e.g., Williams-Guillén et al. 2008), seed dispersal, pollination (e.g., Rocha et al. 2006), soil fertilization, food provisioning, and guano production. Yet bats also have significant negative impacts on societies; for example, disease transmission from bats to humans and livestock is a particular concern (Calisher et al. 2006). Economic valuations of bat behavior have ranged from million dollar gains for pest control services to comparable losses from rabies transmission to cattle by the common vampire bat (*Desmodus rotundus*; Arellano-Sota 1988, Cleveland et al. 2006).

Reciprocally, human behavior has important consequences for bat populations. Out of 1150 recognized bat species, 172 species (15%) are threatened with extinction (IUCN 2012). Habitat loss and roost disturbance are the most commonly cited threats. Many bat species form daytime aggregations within hollow trees, caves, and man-made structures, and these aggregations range from a few individuals to massive colonies numbering in the millions. Due to their high concentrations and absolute abundances, bat aggregations are particularly vulnerable to disturbance when they are discovered by humans (McCracken 1989). Ongoing deforestation is reducing and fragmenting bat habitat; increasing pesticide application threatens bat health and population viability; and direct killing and roost destruction are indiscriminately reducing populations (reviewed by Mickleburgh et al. 2002).

In this study I focused on human-bat interactions in a small, agricultural county in southern Costa Rica (Figure 4.1). Coto Brus County comprises less than 1% of Costa Rica's population (INEC 2012). Prior to the failure of the International Coffee Agreement in 1989 (see Section 4.3.3), most households produced sun-grown coffee on small parcels of land. Coffee production continues today, but low prices and migration of family members to San José and the United States have caused many farmers to move to more extensive, lower input agriculture - particularly cattle production (Rickert 2005). As in other parts of Latin America, bats likely provide a net benefit for many of Coto Brus's farmers (especially coffee producers) and a net loss for others (such as cattle producers; see Section 4.3.4).

The objectives of this study were to learn about the perceptions, knowledge, and interactions that rural people in Coto Brus have with or about bats. The overarching question of this research was: Why do some people in southern Costa Rica kill bats? To evaluate the relative importance of different influences on whether or not people kill bats, I used a conceptual model based on the theory of reasoned action paired with structural equation modeling of survey data (Figure 4.2). The theory of reasoned action is a model of the psychological determinants of human behaviors (Fishbein and Ajzen 2010). Under this framework, an individual's behavioral intentions and actual ability determine his or her behavior. Behavioral intentions are guided by considerations about the outcomes of a behavior, social pressures, and factors that make a behavior easier or more difficult to perform.

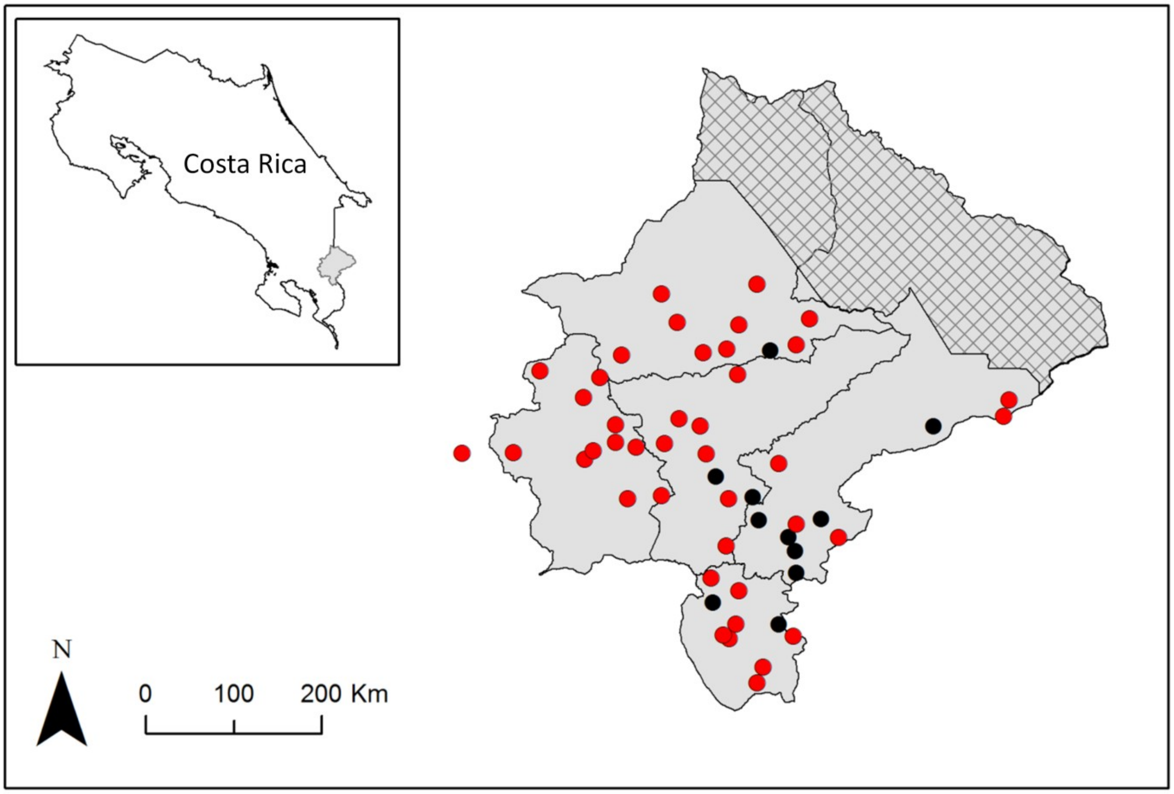

Figure 4.1. Coto Brus County, Costa Rica. Points represent surveyed communities. Red points denote communities where respondents reported problems with vampire bats. One sampled community was outside of the study area but was sufficiently similar to warrant inclusion. Cross-hatching denotes La Amistad International Park.

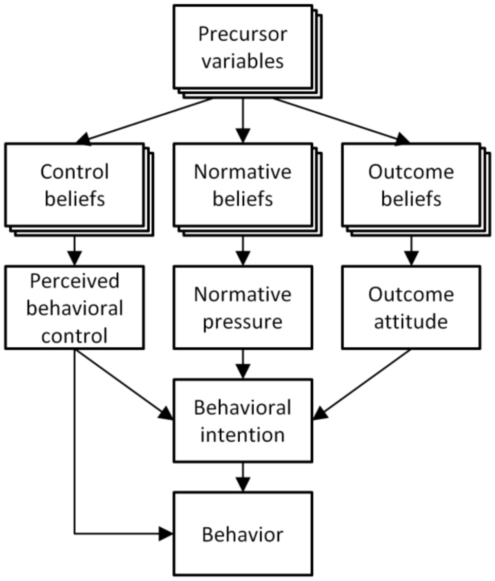

Figure 4.2. Reasoned action model of the determinants of behavior. Operational definitions for each variable are provided in Table 1. The arrow connecting perceived behavioral control to behavior represents an imperfect but realistic measurement of the actual control that an individual has over his or her behavior. Feedbacks from behavior to antecedent variables are not shown, but are inherent in the structure of the theory as outcomes of previous actions can play a major role in determining attitudes and beliefs about behaviors.

4.3. Background

Coto Brus County is a small, rural, inland county in southern Costa Rica situated in the western half of the Generál-Coto Brus Valley on the border with Panama. Dominant topographic features include two mountain ranges, the Cordillera Talamanca (3000 m) and the Fila Cruces (1600 m). Precipitation across the area is variable (~4 m y^{-1} at Las Cruces Biological Station, 1200 meters above sea level on Fila Cruces) but there is always a distinct dry season from December to March. The dominant ecosystem type is tropical premontane humid forest (Holdridge et al. 1971). Currently the county is a patchwork of coffee plantations in the lower and drier areas and cattle pastures on the steeper, wetter slopes. At least 60 species of bats occur in the county (LCBS 2012), and several large bat colonies in or adjacent to Coto Brus are well-known to local people but unprotected.

Costa Rica's 2011 census indicated that Coto Brus contains 38,453 residents (50% women; INEC 2012). Most residents (93%) consider themselves white or mestizo. The majority of residents (77%) live in rural areas, and households have an average of 3.5 members. Most households have basic amenities such as electricity (97%), running water from an aqueduct (88%), and toilets connected to a septic tank (90%). The literacy rate is 95%. Eighty nine percent of the population has at least some primary education; 8% has some university education. Per capita income for Coto Brus is not available from the national census (see Section 4.5.1).

4.3.1. Indigenous People

Indigenous people have likely been present in southern Costa Rica for most of the past 6,000 years. In Costa Rica's 2011 census, 8.9% of people in Coto Brus County self-identified as indigenous. The only indigenous group today is the Guaymí (or Ngäbe). The Guaymí speak Ngäbere, a language in the Chibchan language family (Quesada 2007). As of the 2011 census there were at least 3,400 Guaymí in Coto Brus, however the larger part of the population lives in western Panama and there is significant seasonal migration between the countries. The total population of the Guaymí is probably about 150,000 (Hoopes and Fonseca Z. 2003). Many Guaymí live on one of 22 indigenous reservations in Costa Rica (Stocker 2005).

During Philip Young's fieldwork in 1964-65, Guaymí sociopolitical structures were relatively decentralized, and shifting cultivation was the predominant mode of subsistence agriculture (Young 1971). Marriages at that time were arranged by the fathers of the husband and wife. After a prolonged courtship, the wife usually moved into the house of the husband. With the development of the frontier in western Panama and adjacent Costa Rica in the 1950s-80s, land available for shifting cultivation became scarcer, and fallow periods were shortened. This pressure resulted in Guaymí supplementing subsistence farming with wage labor, particularly on coffee farms, and increased demands on time damaged social networks based on reciprocal assistance (Bort and Young 1985). In 1985, cattle production for the Guaymí was considered a limited foray and represented an ideal but unattainable integration into the national economy (of Panama) for many families. I have found no discussion of bats in any ethnography of the Guaymí.

4.3.2. European Settlement

Although Costa Rica became independent in 1821, the Coto Brus valley was largely uninhabited by Europeans for another 120 years due to a lack of natural resources and remoteness from the major population centers of San José and Panama City. National ownership of the area was disputed by Costa Rica and Colombia (Panama after 1903) until 1941 when U.S.-led negotiations permanently established Costa Rica's sovereignty (Edelman and Seligson 1994).

The first significant wave of non-indigenous migrants to Coto Brus began in the early 1950s and included displaced yeoman peasants from the Central Valley and Guanacaste, immigrants from war-torn southern Italy, and well-connected gentry from San José and abroad. The realization by the small 19th Century Costa Rican aristocracy that coffee could be a lucrative cash crop coincided with the country's independence from Spain. Free from taxation, the aristocracy legislated its way into a coffee-based economy with increasing profit margins and decreasing exposure to risk from the farmer to the exporter to the importers in Europe. Small Central Valley farms were concentrated into larger plantations, but this acquisition resulted in remarkably few violent uprisings compared to other parts of Central America. The peaceful transfer of lands from small farmers to large plantations was facilitated by several factors, including the existence of the Southern Frontier of Coto Brus, which served as a pressure release by allowing many displaced farmers to escape from the hardships brought on by agrarian capitalism. Mitchell Seligson (1980) has contrasted the relatively peaceful movement of peasants from the Central Valley of Costa Rica to the Southern Frontier to the uprisings of the Mexican Zapatistas, who did not want to resettle and instead rebelled. A long series of homestead acts by the Costa Rican government made this out-migration from the Central Valley possible. For instance, a peasant who cleared 10 ha of forest was rewarded with 10 more ha of forest.

By the early 20th century there was a large contingency of landless peasants eager to settle the developing frontier. These aspirations were fueled by the expectations that Coto Brus would become a hub of international commerce when the Pan-American Highway was constructed and that there would be a large market for farm produce in the United Fruit Company banana plantations in the lowlands around Golfito (Edelman and Seligson 1994). These colonists were often very poor and would walk or ride horses over the cold Cerro de la Muerte and then down to San Isidro at the northwestern edge of the Generál-Coto Brus Valley. From here the colonists would enter the forest and walk for perhaps 100 kilometers until they located a patch of ground flat enough to build on. These lands were still covered in old-growth forest, which had to be cleared by hand (Cole-Christensen 1997).

Poor settlers were joined by well-connected urbanites from San José who collectively acquired almost half of the land in Coto Brus County (about 40,000 ha) on a total of four properties by 1955. The owners of the properties were mostly absent, and untitled farmers already occupied much of the land that they claimed. By the 1980s this situation led to widespread squatting and some outbreaks of violence (Edelman and Seligson 1994).

An additional 10,000 ha of land were granted to the Societá Italiana di Colonizzazione Agrícola in 1951, led by Vito Sansonetti (Edelman and Seligson 1994). The Costa Rican government used the promise of the Pan-American Highway to attract the Italians. They sold the land cheaply with the expectation that the Italian immigrants would develop the regional infrastructure. Most of the colonists came from southern Italy, which was devastated during 1943-1944 when Allied forces landed on the toe of the peninsula and fought their way to Rome. Colonization of Coto Brus by Italians was likely motivated by the bleak, post-war economy and high unemployment in Italy.

Early migrants were soon joined by large numbers of squatters. Unemployed workers came from the banana plantations around Golfito to harvest coffee in Coto Brus and stayed on, occupying much of the land titled by absentee owners. Some of the squatters were well organized, and gradually the large properties were split up either through deals with squatters or government expropriation (Edelman and Seligson 1994). Pro-squatter laws were a legacy of the colonial period in Costa Rica when land was so abundant it was considered worthless. The persistence of the laws into recent times is probably due in large part to the 1942 *Ley de Ocupantes en Precario*. This law provided relief to landowners in the Central Valley whose land had been squatted on by allowing owners to exchange their farm for an amount of land of equal value elsewhere in the country. In many cases this was an excellent deal because a small amount of land in the Central Valley was worth many times its acreage on the Southern Frontier. Nonetheless, Seligson (1980) points out that the life of a Costa Rican squatter was characterized by uncertainty and insecurity.

Importantly, much of the claimed land in southern Costa Rica was never officially titled. Without title, landowners are ineligible for bank credit, and other methods of capital accumulation must be pursued in order to make farm improvements. Land titling was both low on the list of priorities and prohibitively expensive for many early settlers as they arrived in Coto Brus, carving a homestead from the old-growth forest (Cole-Christensen 1997). Subsequent transactions were equally informal – at least one long-time resident of San Vito recalls using a cigarette paper as a bill of purchase (Edelman and Seligson 1994). As of 1980 it was estimated that as much as one quarter of all land in Costa Rica was untitled and possibly as much as 91% in remote areas (Seligson 1980). The resultant lack of bank credit has important implications for the value that people may attach to their livestock - a focal point of human-bat conflict in the region. While 30 years have likely improved the land tenure situation, many lands near the Panamanian border remain untitled.

4.3.3. Coffee Production and the Coffee Crisis

Since the 19th century, coffee has been of central importance to the Costa Rican economy, and the state has routinely pushed landowners towards its production. As early as 1821, free coffee seedlings were given to any individual willing to plant them, and some cities even required families to plant it (Seligson 1980). As a crop, coffee was well suited for Costa Rican farmers because it was labor- rather than capital-intensive, it could be grown on steep slopes, and once abandoned it could be easily rejuvenated. However, coffee is also an inelastic commodity that cannot be eaten during hard times (Sick 1999).

Institutional changes over the past 25 years caused the price of coffee paid to farmers to drop precipitously and become more volatile. These changes revolved around the termination in 1989 of a quota system called the International Coffee Agreement. The resulting shift increased the power of roasters relative to traders, exporters, and producers, and a large share of overall coffee profits moved from local farmers to large corporations in consumer (*i.e.*, northern industrial) countries. The problem was exacerbated by a consistent oversupply of low-quality coffee beans, which may be seen as an inevitable result of a global system that encourages planting in some years, when the market is good, and discourages reducing production, since coffee is a perennial crop (Ponte 2002).

Impacts of the coffee crisis can be readily seen in contemporary farms in Coto Brus. One survey of 59 farming families found that 76% of farmers reduced their acreage of coffee between 1998 and 2003 (Rickert 2005). Of those that reduced coffee, 93% attributed this decision to low coffee prices. Sixty four percent of this land was converted to cattle pasture, and 14% was abandoned outright.

Land use changes resulting from the coffee crisis likely shifted the balance of environmental services and disservices flowing from bats to people. Coffee farmers, in contrast to cattle producers, receive a net benefit from having bats on their farms, although that benefit is frequently unrecognized. A study in coffee farms in Mexico found that bats significantly reduced the abundance of herbivorous arthropods on coffee trees (Williams-Guillén et al. 2008). Similar results have been found in tree plantations in Coto Brus (Morrison and Lindell 2012), and studies in natural communities suggest that such reductions in herbivores reduce leaf damage and increase plant growth (Marquis and Whelan 1994, Kalka et al. 2008). When coffee producers converted their plantations to cattle pastures, herbivorous pest control became voided as a benefit and was likely supplanted by an increasing population of common vampire bats.

4.3.4. Cattle Production

Increasing cattle production is a relatively recent trend in Coto Brus, a county that was completely dominated by coffee plantations 20 years ago. The reasons for abandoning coffee have already been explained, but why have so many farmers replaced their coffee with cattle? Following the coffee crisis, governments throughout Central America created programs to help farmers diversify their means of production. Typically, "diversification" meant cattle ranching (Dicum and Luttinger 1999, Rickert 2005). Cattle ranching requires considerably less labor and investment than coffee production. Following the coffee crisis, producers were unable to pay for labor, and this may have made cattle production more attractive. Eve Rickert (2005) has also suggested that the low investment cost of cattle ranching may have attracted former coffee farmers, particularly those with limited access to credit markets.

For some farmers there may be few alternatives to cattle production. Terrain in Coto Brus is typically steep, high in elevation, and wet. As such, lowland plantation crops such as oil palm, cacao, banana, and pineapple are not practical to cultivate. Some households have begun growing peppers and tomatoes for export, but high rainfall in Coto Brus (~4 m yr^{-1}, locally variable) makes these very intensive crops; to prevent damage from the frequent rains, farmers must cover each row of crops with taut plastic sheets. Most farmers are engaged in some home gardening, but a move towards subsistence farming is unlikely.

Means of capital production are limited not only by the physical environment and access to markets but also by the skills and experience of individuals. Many families that migrated to Coto Brus came from Guanacaste, which is traditionally a cattle ranching province (Helmuth 2000). With the failure of coffee, it is not surprising that smallholders who were able to afford cattle adopted that strategy.

Whereas coffee production is labor intensive and capital extensive, cattle production is the opposite. The increasing ability of individuals to invest in cattle – and their decision to do so – may be due in part to the fact that some families now receive remittances from family members who have become migrant laborers (de Sherbinin et al. 2007). Equally important, the net emigration of young people from Coto Brus (e.g., Kutsche 1994) has decreased the labor force and increased the average age of farm workers. Both of these changes predict that remaining farmers would seek methods of production that require as little manual labor as possible.

Pastures are not the only place in Coto Brus that one sees cattle. Walking down a rocky country road, one sees many cattle tethered to fence posts and trees eating the roadside vegetation. The density of these cattle is never high, suggesting that this is a feeding strategy used for one or two family cows and not for a large-scale cattle operation. Recall that without land title, access to credit from banks is unavailable (Seligson 1980). Thus, cattle production by unlanded families or households with untitled land may be conceptualized as a form of rural banking.

If cattle represent a primary means of production or a form of household savings, then people who own cows will likely act to minimize risk to that investment. Damage incurred by the common vampire bat represents one such risk. Vampire bats have a variety of unique adaptations for feeding on blood (Brown 1999), and today most vampire bats specialize on the blood of livestock (Voigt and Kelm 2006). By creating open wounds on cattle and other animals, vampire bats facilitate infection and parasitism (*e.g.*, screwworms). Vampire bats are also a primary reservoir of rabies (Streicker et al. 2012). An untreated epidemic of bovine paralytic rabies (*i.e.*, rabies that affects cattle) can cause 30-50% herd mortality, representing a significant threat to cattle producers (Constantine 1970). Acha and Arambulo III (1985) estimated that bat-transmitted rabies accounted for the annual death of approximately 100,000 cattle in Latin America (out of 70 million total), with an overall cost of $30 million per year. The extent to which cattle producers are vulnerable to such risks is variable and depends in part upon the proximity of forest and the density of livestock in the surrounding landscape (Gomes et al. 2010) as well as the relative importance of cattle to the livelihood of the owner. Governments and individuals have attempted to control vampire bat populations with a range of methods, some inexpensive and indiscriminate (e.g., dynamite). Other methods are less destructive and more effective (see Section 4.6.3), but also require more resources and technical capacity (Greenhall 1974, 1985).

4.3.5. Historical Context Contributing to Human-Bat Conflict

Land use changes since 1941 have made Coto Brus a relevant location for identifying determinants of bat killing behavior. Starting with the influx of European-descended pioneers from the Central Valley, indigenous resource management systems were undercut. Old-growth forest and land that had historically been used by the Guaymí for rotational agriculture were converted to coffee plantations. Whereas a combination of old-growth forest, subsistence agriculture, and coffee cultivation likely supported a diverse community of bats with a relatively low abundance of vampire bats, the social system underlying this landscape was unstable. Old-growth forests and fallow areas continued to be seized and cleared through the 1980s, and by 1994 only about a quarter of the county remained forested (Daily et al. 2001). In 1989 the International Coffee Agreement failed, and many farmers converted their coffee plantations to cattle pastures (Rickert 2005). During the transition, many or most households had no access to bank credit, and banking in cattle may have been a means of saving wealth.

As cattle density increased on the Coto Brus landscape, marginal agricultural lands were also abandoned, leading to the regrowth of secondary forests. Common vampire bats roost in forests and feed primarily on livestock (Voigt and Kelm 2006), and a study in São Paulo, Brazil found that forest cover and cattle density were the most important predictors of vampire bat attacks in that region (Gomes et al. 2010). Given these trends, it seems possible that there is a latent risk of human-bat conflict in southern Costa Rica. A trigger, such as a rabies episode, could lead to significant bat persecution (Hutson et al. 2001).

4.4. Methods

I used qualitative and quantitative methods in a two-step process of survey development. First, I sought to better understand the local context for human-bat interactions using focus groups, a natural history survey, and interviews with local informants. Second, I used a pilot survey to identify common beliefs about killing bats. The survey was used to collect quantitative data for a conceptual model based on the theory of reasoned action (Figure 4.2).

4.4.1. Survey Development

I conducted a series of interviews in February 2011 to evaluate local perceptions, knowledge, and interactions with bats. I first conducted four focus groups (Krueger and Casey 2000) with men and women from two communities: Ceibo, an agricultural community near the urban center of Sabalito, and Pittier, a small town on the edge of La Amistad International Park. Focus groups consisted of 3-7 informants (N = 21 total participants) who were asked to discuss their knowledge of and interactions with bats starting from prompts such as *What have you heard about bats?* and *How do bats affect your life?* (Appendix 1). Informants were identified and invited to participate by local contacts in each community, and a native Spanish speaker, C. Vindas-Chavez, facilitated.

As a second measure of regional bat knowledge, I conducted a brief natural history survey. I used flash cards with bat illustrations (Bonaccorso 1998, Reid 2009a) to facilitate questions such as *What do you call this animal?*; *What do these animals eat?*; and *Which of these animals have you seen around here?* (Appendix 2).

Informants came from four of the five districts of Coto Brus (Agua Buena, Limoncito, Sabalito, and San Vito) and included 22 women and 14 men.

To learn about local environmental education efforts and available methods for managing vampire bat damage to livestock I interviewed several key informants including a representative of the Ministry of Agriculture and Cattle (MAG), two environmental educators, and six veterinarians. Interviews were semi-structured and included questions about where people have problems with vampire bats, what services or products are recommended for managing vampire bat damage, and what bat-specific environmental education has been offered in Coto Brus.

To identify important beliefs for inclusion in a final survey instrument, a pilot survey administered by C. Vindas-Chavez was undertaken of 30 men (5-6 per district) in Nov-Dec 2011 (Appendix 3). Only men were surveyed because focus group interviews suggested that men are far more likely than women to encounter and kill bats outside of the home (see Section 4.5.2). Informants were asked what they would do if they found bats roosting on their farm. Then they were asked to list: (1) advantages and disadvantages of killing bats; (2) people who would approve or disapprove of killing bats; (3) people whose opinions influence their decisions about farm management; and (4) factors that make it easier or more difficult to kill bats (Appendix 3). Common responses from these open-ended questions were used to form closed survey items for the final instrument. Incomplete capture of important beliefs in the pilot survey has the potential to reduce the predictive power of a final model, but too many survey items reduce participation. I balanced these concerns by selecting a pool of common attitudinal and normative beliefs from the pilot survey that accounted for at least one opinion of at least 70% of the 30 informants.

I excluded from the final survey items related to beliefs about self-efficacy and perceived control. In doing so, I assumed that bat killing is not constrained by a lack of resources, capabilities, or self-efficacy. This assumption was supported by pilot survey results and by information about local context. When pilot survey respondents were asked what makes it easier or more difficult to kill roosting bats, 11 (37%) informants reported that killing bats is easy (*i.e.*, there is nothing difficult about doing it). An additional 11 (37%) reported that locating roosting bats makes killing them more difficult, but the final survey precludes this difficulty by presenting a hypothetical situation in which the respondent has found a bat roost in a hollow tree. Fifty percent of informants reported that commercial bat poison makes it easier to kill bats, but given that this is a cheap, uncontrolled, widely-available substance, it did not seem like access to poison would significantly limit bat killing. Collectively, these three beliefs accounted for 80% of informants. I nonetheless included one item in the final survey to assess overall ease or difficulty of bat killing and ensure that an important theoretical component was not overlooked.

4.4.2. Survey

To evaluate the determinants of bat killing behavior among men in southern Costa Rica, I developed a survey based on the theory of reasoned action. The theory of reasoned action can be described mathematically (Ajzen 1991):

$$BE \sim BI \sim \beta_1 OA + \beta_2 NP + \beta_3 PC = \beta_1 \sum_{i=1}^{k} OB_i OE_i + \beta_2 \sum_{i=1}^{m} NB_i MC_i + \beta_3 \sum_{i=1}^{n} CB_i PO_i$$

where behavior (*BE*) is a function of behavioral intention (*BI*), which is determined by outcome attitude (O*A*), normative pressure (*NP*), and perceived behavioral control (*PC*). Each of these three constructs is determined by the sum of products of beliefs (*OB*, *NB*, *CB*) times their stated importance (*OE*, *MC*, *PO*). Precursor factors such as demographics are presumed to mediate behavior via their influence on individual beliefs. Operational definitions for each variable are given in Table 4.1.

An important assumption of this model is that behavioral intentions are reasonable predictors of actual behavior. A meta-analysis of 175 studies using this basic framework found that an average of 39% of variation in behavioral intentions was explained by outcome attitudes, normative pressures, and perceived behavioral control. Importantly, studies using this framework successfully have included negative behaviors (*e.g.*, drug use; Orbell et al. 2001); dishonest behaviors (e.g., lying, cheating, and stealing; Beck and Ajzen 1991); and sensitive behaviors (*e.g.*, handwashing by nurses; Whitby et al. 2006). In many cases, including bat killing, observing actual behavior is not feasible and behavioral intention is the closest approximation possible. For this study, I used self-reported bat killing behavior over the previous five years as a best-approximation measure of actual behavior. The implications of using self-reported behavior are discussed in Armitage & Conner (2001).

To collect quantitative data to inform the conceptual model, 504 surveys were administered to men in 50 towns (10 per district) in each of the five districts of Coto Brus (Appendix 4). Towns were selected randomly, and households within towns were selected haphazardly by choosing a rural street and visiting each household along the street until the quota was reached. This design may have introduced a sampling bias based on proximity to towns and reflects limitations in the study area (see Section 4.4.3). Only one man per household was interviewed, and surveys were administered by native Spanish speakers.

Participants were asked 48 questions, 47 of which were closed-ended. The survey included five natural history items, 34 theory of reasoned action items, and nine precursor variable items. Precursor variables included demographics, natural history knowledge, an index of relative house quality, and whether or not respondents had access to credit, worked on a farm, grew coffee, raised cattle, or had problems with vampire bats. Natural history items were based on a five-question quiz used at Tirimbina Biological Station to assess the success of bat-related environmental education (E. Cordero Schmidt 2011 *pers. comm.*). The subjective index of relative house quality was used as a proxy for wealth. Reasoned action items were based on common responses to open questions from a pilot survey.

4.4.3. Limitations

My decision to conduct surveys in person rather than by mail reflects two limitations of the study area. First, there are no large accessible repositories of mailing addresses for southern Costa Rica. This is due in part to the fact that Costa Rica does not practice the convention of naming streets or numbering houses. Additionally, a substantial proportion of the target audience for this survey is illiterate or marginally literate, making mail-in surveys suboptimal. A trade-off of using surveying in-person is that the survey needed to be kept short to increase participation and reduce survey administration time. Whereas multiple measures of outcome attitude, normative pressure, and perceived behavioral control would be ideal (Fishbein and Ajzen 2010), I used only one measurement per variable.

Table 4.1. Operational definitions of model parameters and examples of survey items that could be used to measure them. Scales for survey items are on a scale of 1 = strongly disagree to 5 = strongly agree. Items are ordered as they appear in Equation 1.

Variable	Significance	Operational definition
BE	Behavior	Whether or not an individual has killed any bats over the past five years (binary).
BI	Behavioral intention	Likelihood that an individual will kill bats if s/he finds them sleeping in a roost on the farm (positive integer, range 1-5).
OA	Outcome attitude	Favorableness that an individual feels towards killing bats (positive integer, range 1-5).
NP	Normative pressure	Perceived approval or disapproval of bat killing by members of an individual's social networks (positive integer, range 1-5).
PC	Perceived behavioral control	Perceived ease or difficulty of killing bats (positive integer, range 1-5).
OB	Outcome belief	A belief held by an individual that is relevant to his attitude about bat killing (positive integer, range 1-5). Ex: *Killing bats could reduce damage to my livestock and domestic animals.*
OE	Outcome evaluation	Favorableness of an expected outcome (positive integer, range 1-5). Ex: *The health of my livestock and domestic animals is important to me.*
k	Number of outcome beliefs	Number of relevant outcome beliefs needed to understand the formation of an outcome attitude.
NB	Normative belief	A belief held by an individual about the approval or disapproval of another person or group regarding bat killing (positive integer, range 1-5). Ex: *Members of my family would approve of me killing bats.*
MC	Motivation to comply	Importance associated with a given person or group's opinion regarding bat killing (positive integer, range 1-5). Ex: *The opinion of my family members about whether or not I kill bats is important to me.*
m	Number of normative beliefs	Number of relevant normative beliefs needed to understand the formation of perceived normative pressure.
CB	Control belief	A belief held by an individual relating to the ease or difficulty of killing bats (positive integer, range 1-5). Ex: *Costa Rican law makes it difficult for me to kill bats on my farm.*
PO	Power of control belief	Degree to which a control belief facilitates or inhibits the killing of bats by an individual (positive integer, range 1-5). Ex: *I can kill bats without legal repercussion.*
n	Number of control beliefs	Number of relevant control beliefs needed to understand perceived behavioral control.

4.4.4. Data analysis

I used structural equation modeling to analyze a conceptual model of the determinants of bat killing behavior (Figure 4.2). I divided the model into three sections and analyzed each of them separately. As a general strategy, I started with models that included all relevant beliefs and precursor variables and then removed unimportant predictors to derive the most parsimonious solutions. Total effects of individual beliefs and precursor variables on outcome attitudes, normative pressure, and behavioral intent were calculated using Wright's (1960) tracing rules for path analysis (Grace 2006). Data typically violated the assumption of multivariate normality (Shapiro-Wilk tests, all $P < 0.05$), so I used robust methods for each analysis. Models were assessed using the lavaan package (Rosseel 2012) in R.2.15.2 (R Development Core Team 2012).

I first tested a model of the direct determinants of the theory of reasoned action, including self-reported bat killing behavior (*BE*), behavioral intention (*BI*), perceived behavioral control (*PC*), normative pressure (*NP*), and outcome attitude (*OA*). I treated self-reported bat killing as a binary variable (0 = no kill, 1 = kill) and used diagonally weighted least squares regression.

Second, I tested a model for the outcome attitude arm of the theory of reasoned action, linking precursor variables to outcome attitude (*OA*) via relevant beliefs (*OB1-3*) and expectations (*OE1-3*). For each outcome belief and expectation, I multiplied *OB* × *OE* to produce a single variable (range 0-25) representing the overall importance and valence of a given belief. After estimating an initial model, I removed precursor variables that did not significantly predict at least one of the three beliefs at a level of $\alpha = 0.1$. I estimated the reduced model and calculated the total effects of each precursor variable on outcome attitude (*OA*), then simplified the model again by including only the two precursor variables with the greatest standardized total effects.

Third, I modeled the normative arm of the theory of reasoned action including precursor variables, normative beliefs (*N1-3*), and normative pressure (*NP*). Belief parameters again represent the product of each normative belief (*NB*) and motivation to comply (*MC*). An initial model was estimated and then simplified using an $\alpha = 0.1$ cut-off. A final model was produced that included only the two most important precursor variables.

For each structural equation model, I report five standard goodness-of-fit statistics: chi-squared (χ^2), comparative fit index (CFI), Tucker-Lewis index (TLI), root mean square error of approximation (RMSEA), and standardized root mean square residual (SRMR). SRMR is not presented for the direct determinants model, which used a binary response variable. None of these metrics is a perfect measure of model fit, and my data were particularly vulnerable to low χ^2 P-values as a result of having a large sample size.

To evaluate practical implications of this work, I compared natural history scores among respondents with varying levels of exposure to environmental education (none, classroom experience only, classroom experience and television programs, and television programs only). I also compared planned bat killing behavior among respondents with and without a bat-related environmental education experience of any kind (classroom or television) and with and without experience with vampire bats attacking livestock. For the first test I used a one-way analysis of variance and Tukey post-hoc pairwise comparisons. For the second I used a two-way analysis of variance. For both tests $\alpha = 0.05$.

4.5. Results

4.5.1. Demographics

The survey population for this study was predominantly middle-aged (mean 48 ± 1 years SE, range 18-86, N = 501), and ages were normally distributed. Spanish was the primary language of 96% of respondents; three percent spoke an indigenous language (Guaymí or Ngäbere), and one respondent each spoke English or Italian. Mean 2011 income was $4411 ± 145 USD (N = 431), and income distribution was skewed to the right. Twenty-five percent of respondents had bank credit. Eighty one percent of respondents worked on a farm; 45% produced coffee, 46% produced cattle, and 20% produced both.

4.5.2. Human-Bat Interactions

Focus group interviews highlighted three main contexts in which men and women in Coto Brus interact with bats: (1) when bats enter a house; (2) when bats attack farm animals; and (3) when bats attack humans. The latter circumstance was infrequent and told as hearsay rather than personal experience. For instance:

> One has heard that in the past the people were very poor and slept without blankets, so the children would wake up bitten [by vampire bats]. Everyone walked with a limp. Since it's cold here, everyone now sleeps with a good blanket, but in the past [vampire bats] bit people every day.

Reported conflicts between bats and livestock consisted of vampire bats feeding on cattle and chickens. Consequences of this interaction included weakening of calves and killing of chickens. One respondent said that his neighbor could no longer keep chickens because bats always kill them. Disease transmission was sometimes mentioned as a consequence of vampire conflict. Responses to vampire bat depredation of livestock ranged from the application of a pesticide, Warfarin, to hanging garlic cloves around a cow's neck to ward off vampires (Table 4.2). A woman in Pittier summarized many of the concerns about vampire bats and livestock:

> When they suck the blood of the cow and debilitate them it is bad, because cattle are expensive, and they come to an animal and keep coming. The cow goes anemic and the chickens die.

Five out of six local veterinarians and a representative of the Ministry of Agriculture and Cattle (MAG) confirmed that vampire bat damage to livestock is a problem in Coto Brus. These informants suggested that vampire bat problems are most common in low-lying parts of the county near rivers (3/7 informants), though a larger survey suggested that vampire conflicts are more widespread (Figure 4.1). The most common recommendations for farmers with vampire bat problems were to apply Warfarin, a blood thinner, to a cow's wounds (5/7 informants) or add sulfur powder to their food (4/7 informants; Table 4.2). A MAG representative told me that prior to 2006 farmers could contact MAG, which would send an employee to a farm to catch bats in mist nets and apply Warfarin to vampire bats directly - a method that effectively controls vampire bats without harming other species (Greenhall 1974). This service was discontinued in Coto Brus due primarily to the cost of purchasing new mist nets.

Human-bat interactions were strongly divided by gender. In focus groups men tended to discuss encounters with bats on the farm and conflicts between vampires and livestock, whereas women talked about dealing with bats in the house, sometimes by shooing them out with a broom. These divisions were not universal; one man, for example, let his cat deal with bats in his home:

> ...[bats only affect me] when they get into the house to be an annoyance. When that happens I turn on the light so that they go down to the floor, and the cat takes care of the little bat.

Most people reported that they had seen bats inside of their own house or another house, especially old, dark houses. They said that bats come in to roost and people find dozens or hundreds hanging from the ceiling. In other cases, bats will fly in through an open window or will come into the kitchen to eat bananas or plantains. Sometimes people will poison bananas or sugar water in order to kill them.

Table 4.2. Methods for controlling vampire bats that were suggested or implemented by veterinarians, farmers, and agricultural extension agents in Coto Brus. Methods are sorted by relative frequency. Sources: CO = information based on conversations with local people; FG = focus groups; I = interviews with veterinarians and an agricultural extension agent.

Method	Frequency	Source
Tie a red cloth around the neck of a cow that has been bitten by a vampire bat	Common, but sometimes referred to as a belief rather than a real solution.	FG, CO
Rub poison (Warfarin) around cow's wound	Suggested by 5/6 vets. Uncommonly implemented by respondents.	FG, I
Add sulfur powder to cattle food supplements	Suggested by 4/6 vets. Only reported as implemented by one respondent.	FG, I
Consult the MAG (Ministry of Agriculture and Cattle)	Suggested by 3/6 vets.	I
Inject cattle with Ivermectin	Implemented by some men in a remote township with large farms. Ivermectin treats parasites that may infect wounds opened by vampire bats.	FG
Capture bats with mist-nets and apply Warfarin directly	This method was recommended by 3/6 vets. Only one respondent had a vague recollection of this procedure, which has been unavailable in Coto Brus since at least 2006.	FG, I
Apply Warfarin to bananas and leave out for bats to consume	Implemented by one respondent. This method certainly kills fruit bats.	FG
Rub lemon on the back of the animal	Implemented by a single respondent, who admitted that he did not know what the result could be.	CO
Rub burned motor oil on the cow	Implemented by a single respondent.	CO
Pen cattle and shine bright lights on them	An agricultural extension agent suggested this impractical method.	I
Mix Warfarin into a sugar water solution and leave out for bats to consume	Implemented by at least one farmer.	CO
Hang spikes from the ceiling	Implemented by one respondent, presumably to deter bats from hanging.	FG
Hang garlic around the house to deter vampires	Implemented by one respondent.	FG

A third category of human-bat interactions involved bats attacking humans. Several people had heard of others being bitten, often in the historic past, and one man reported having been bitten himself while in the lowlands. One farmer in Pittier said that in the past people put cats in their children's cradles to keep vampire bats away. This type of interaction was infrequent enough that there were no response behaviors that could be directly linked to it.

4.5.3. Perceptions of Bats

Focus group respondents predominantly had negative perceptions of bats. Discussions revolved around negative impacts of bats on their lives. Some men cited fruit-eating and pollination as things that bats do, but in no case did any informant submit a positive effect that bats had on his or her life. Rather, people who were not negatively affected by bats tended to say things like:

> No...no bats do not affect me. Thank God. Everything is good. Everything is fine.

or at best:

> I think that it is not necessary to kill them. If I see one in my coffee plantation, I do not kill it. It is an inoffensive critter. There is no need. It is equivalent to a bird, or something like that.

Hearsay reports of bats attacking humans amplified negative attitudes about them, particularly when combined with the notion that bats spread deadly human diseases. Several respondents discussed rabies transmission by bats, and one woman suggested that bats might also transmit AIDS to humans, though she was uncertain.

4.5.4. Knowledge about Bats

Out of 36 respondents to a brief natural history survey, most described an illustration of a common fruit bat (*Carollia perspicillata*) as a "bat" (*murcielago*; 69%), but a significant minority called it a "vampire" or "blood-sucker" (*vampiro* or *chupasangre*; 36%), and two respondents confused it with an armadillo (*cusuco*; 6%; Figure 4.3). Likewise, only one respondent correctly identified a common vampire bat from a series of illustrations of ten bat species. Respondents more often selected a non-native bat (*Hipposideros diadema*; 11%); a common sentiment was that the vampire must be the biggest or the blackest bat in the group. Collectively, respondents produced a comprehensive list of the main types of food consumed by the local bat community, though blood was conspicuously over-represented compared to more commonly-consumed resources such as insects and nectar (Figure 4.3).

The mean score on a second natural history survey was 3 ± 1 correct answers out of five items (N = 501; Table 4.3). Most respondents correctly answered that not all bats are vampires (88%), but only 18.7% correctly answered that bats have five fingers. Natural history scores varied significantly among respondents with different exposure to environmental education (ANOVA df = 3,495, F = 12.9, $P < 0.001$, Figure 4.4), most of which came from television.

4.5.5. Bat Killing

Out of 503 men surveyed, 72 (14%) indicated that they had killed roosting bats over the preceding five years (Figure 4.5), and 134 (27%) said that they would kill bats or set fire to the roost if they found bats roosting on their farm (Table 4.4). Three hundred and forty three respondents (68%) said they had killed bats when they were children (N = 503).

A structural equation model of the direct determinants of bat killing behavior provided a good fit to the data (χ^2 $P = 0.159$; CFI = 0.996; TLI = 0.987; RMSEA = 0.041; Figure 4.6, Tables 4.5-4.6). Intention to kill bats was positively correlated to self-reported bat killing behavior ($R^2 = 0.17$), and outcome attitude had the greatest direct ($r = 0.75$) and total ($r = 0.81$) effects on behavioral intention.

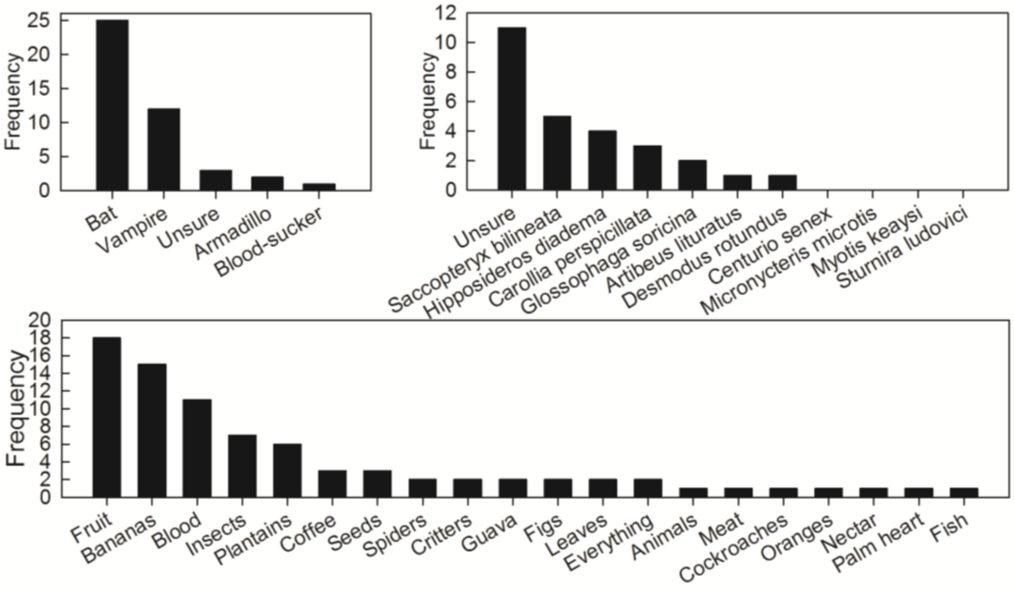

Figure 4.3. Histograms from a natural history survey. (*Top left*) Responses to the question *What do you call this animal?* Respondents were shown an illustration of a common fruit bat (*Carollia perspicillata*). (*Top right*) Responses to the question *Which of these species is a vampire?* Respondents were shown a set of ten illustrations of local bat species including the common vampire (*Desmodus rotundus*) as well as one non-native species (*Hipposideros diadema*). (*Bottom*) Responses to the question *What do these animals* [local bat species] *eat?*

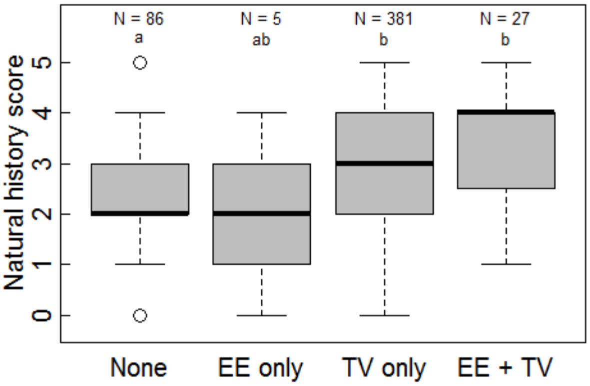

Figure 4.4. Sources of information about bat natural history. EE = environmental education that included information about bats; TV = television. Sample sizes and significant differences (Tukey HSD test, α = 0.05) are given above the boxes. Outliers are shown as hollow circles.

Table 4.3. Natural history survey items and responses. Responses are listed in order of frequency, and correct responses are in bold.

Survey question	Responses	N
To what group do bats belong?	**Mammals (68.7)**, Birds (12.5), Reptiles (3.6)	504
What do bats eat when they are born?	**Milk (50.8)**, Insects (16.9), Blood (14.1)	504
How many fingers do bats have?	Three (33.1), **Five (18.7)**, None (8.1), Two (0.2)	504
What kind of animal eats bats?	**Owl (77.7)**, Crocodile (1.8), Jaguar (1.2)	503
Are all bats vampires that suck blood?	**No (88.0)**, Yes (9.0)	502

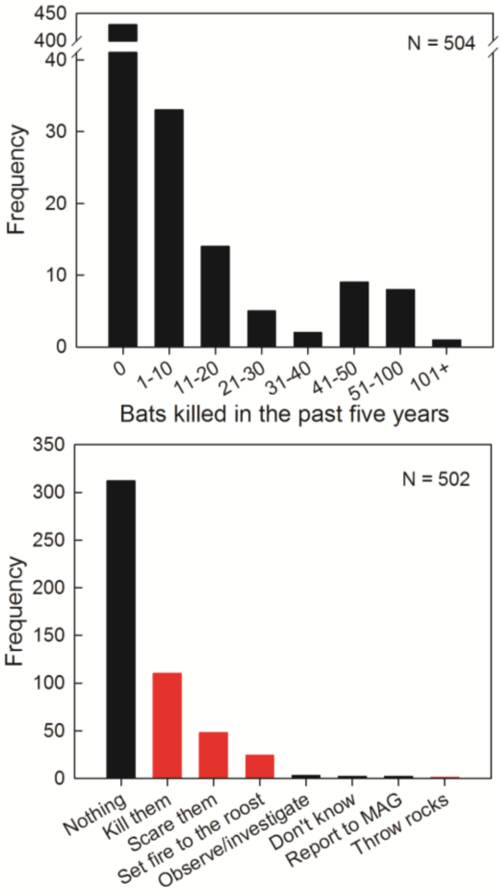

Figure 4.5. Bat killing by men in southern Costa Rica. (*Top*) Bats killed by respondents over the past five years. (*Bottom*) Frequency of responses to the question: If you were walking on your farm and found a tree with a hole and bats sleeping inside, what would you do? Negative behaviors are shaded red.

4.5.6. Outcome Attitude

I identified three outcome beliefs about bat killing that included the views of 73% of pilot survey respondents. The beliefs were: (*OB1*) killing roosting bats could reduce damage and disease in cattle or other animals - 43%; (*OB2*) killing bats could reduce seed dispersal and pollination on your farm - 37%; and (*OB3*) killing bats would be a damage to nature - 10%. In the larger survey, *OB3* (nature) was the most commonly held belief (Table 4.4). Almost all respondents agreed that it was important to maintain livestock health, seed dispersal and pollination, and nature on their farms (≥98%).

A model of relationships between precursor variables, beliefs, and outcome attitude showed that all three beliefs contribute significantly to respondents' attitudes about bat killing (Figure 4.7, Tables 4.5-4.6). During model refinement two precursor variables, natural history score (*NH*) and vampire problems (*VA*), had the greatest predictive power. A simplified model excluding all other precursor variables greatly reduced the Akaike Information Criterion (AIC) score (ΔAIC = 3623) with a minimal increase in unexplained variance for endogenous variables (χ^2 $P < 0.001$; CFI = 0.948; TLI = 0.612; RMSEA = 0.162; SRMR = 0.034).

4.5.7. Normative Pressure

I identified five normative beliefs about bat killing that included the views of 97% of pilot survey respondents. Respondents identified family members (90%), the Ministry of the Environment (MINAE; 23%), others who do the same kind of work (20%), neighbors (17%), and conservationists (10%) as groups that would either approve or disapprove of the respondent killing bats. About 30% of respondents in the large survey agreed that family members (31%), others who do the same work (26%), and neighbors (27%) would approve of them killing bats; almost none agreed that MINAE (4%) or conservationists (3%) would approve (Table 4.4). Of 272 men with children, 50% disagreed or strongly disagreed that their children would approve of them killing bats (neutral = 25%), and 260 (96%) agreed or strongly agreed that their children's opinions about farm management were important.

A model of relationships between precursor variables, relevant beliefs, and normative pressure showed that only three of these groups (family members, others who do the same kind of work, and neighbors) had significant direct effects on normative pressure (Figure 4.8; Tables 4.5-4.6). Two precursor variables, vampire bat problems and natural history knowledge, had the greatest total effects on perceived normative pressure (Table 4.7). Exclusion of additional beliefs and precursor variables greatly improved model fit (ΔAIC = 10422; χ^2 $P = 0.008$; CFI = 0.982; TLI = 0.865; RMSEA

= 0.087; SRMR = 0.023) with minimal change to explained variance for any endogenous variables.

4.5.8. Environmental Education, Vampire Bat Experience, and Planned Bat Killing

Planned bat killing varied according to whether respondents had any bat-related environmental education and whether they had experience with vampire bats attacking their livestock (Two-way ANOVA, df = 500, $F \geq 32$, $P \ll 0.0001$; Figure 4.9).

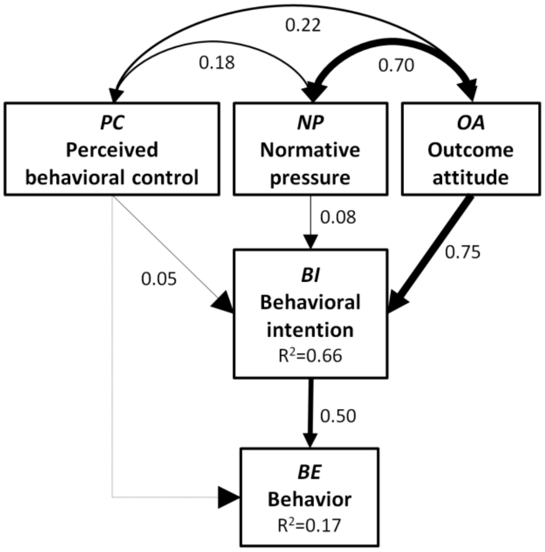

Figure 4.6. Fitted structural equation model of the direct determinants of bat killing behavior. Straight lines represent correlations, and curved lines represent fixed covariances. Dotted lines represent non-significant relationships ($\alpha = 0.05$). Endogenous variables have model fit inside of the box. Line widths are scaled to the partial correlation coefficients. Standardized correlation coefficients are shown.

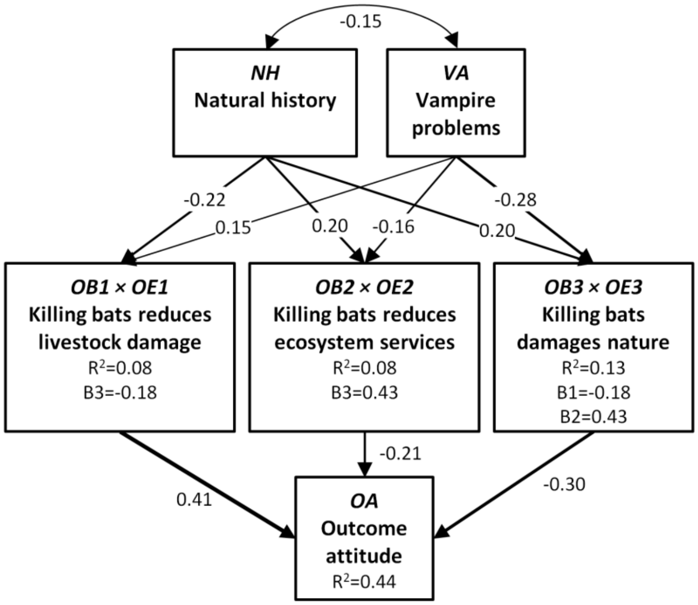

Figure 4.7. Fitted structural equation model of the attitude arm of the theory of reasoned action. Straight lines represent correlations, and curved lines represent covariances. Endogenous variables have model fit inside of the box, and belief variables (*B1*, *B2*, *B3*) also have estimated covariances within the boxes rather than drawn. Line widths are scaled to the partial correlation coefficients. Standardized correlation coefficients are shown.

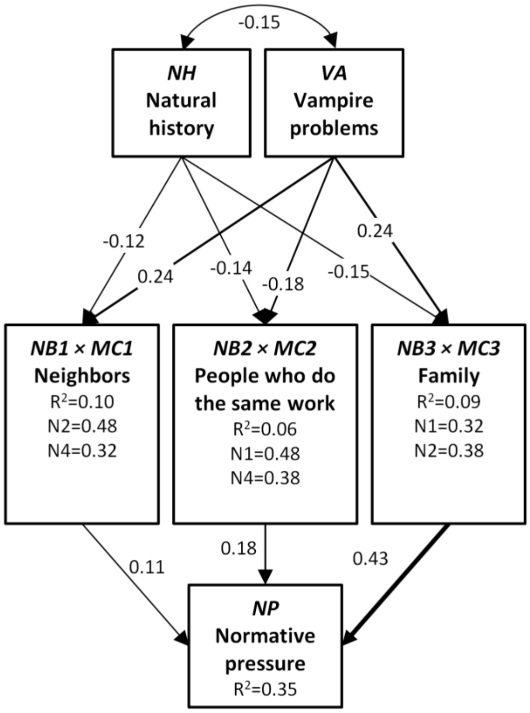

Figure 4.8. Fitted structural equation model of the normative arm of the theory of reasoned action. Straight lines represent correlations, and curved lines represent covariances. Endogenous variables have model fit inside of the box, and belief variables (*NB1 × MC1*, *NB2 × MC2*, *NB4 × MC4*) also have estimated covariances within the boxes rather than drawn. Line widths are scaled to the partial correlation coefficients. Standardized correlation coefficients are shown.

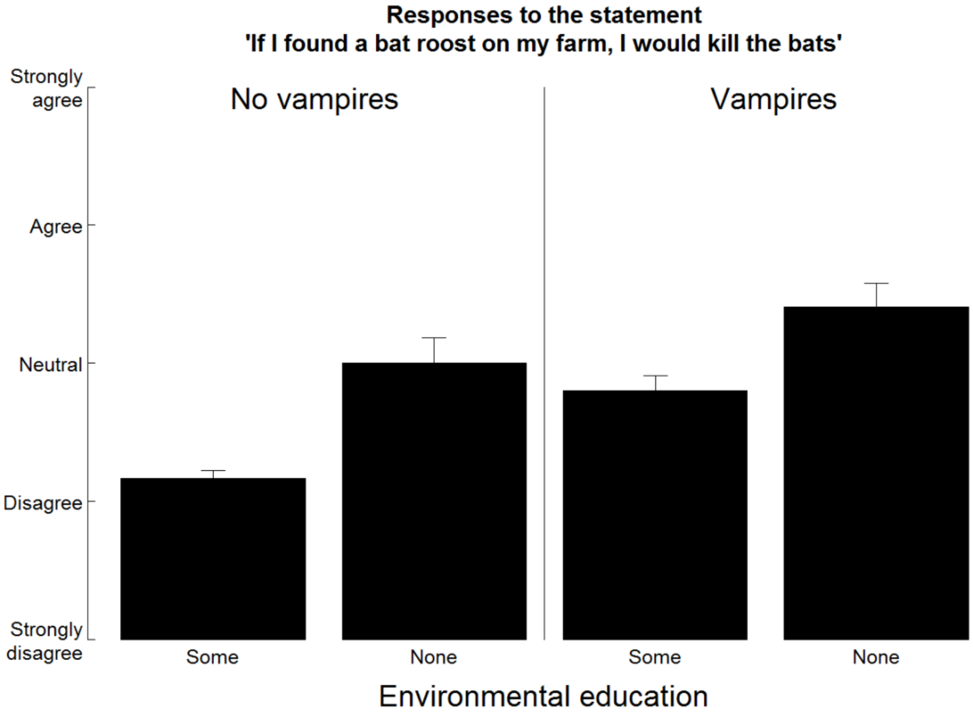

Figure 4.9. Direct correlation between environmental education and experiences with vampire bats on planned bat killing. Both effects were significant (Two-way ANOVA, df = 500, $F \geq 32$, $P \ll 0.0001$).

Table 4.4. Survey items and responses for each model parameter.

Var	Survey item	Agree (%)	Neutral (%)	N
BI	If you find bats sleeping in a tree hollow on your farm, you are going to kill them.	25.2	6.5	504
OA	If you found bats, the best thing for you to do would be to kill them.	30.2	8.7	504
NP	The majority of people whose opinions are important to you would approve of you killing bats if you found them on your farm.	26.0	22.8	504
PC	You have the ability to kill bats if you need to do so.	51.2	3.4	504
OB1	If you kill bats, it could prevent damage and disease for your livestock and other animals.	42.7	22.8	504
OE1	It is important for you to maintain the health of your cattle and domestic animals.	98.8	0.2	504
OB2	If you kill bats, seed dispersal and flower pollination on your farm could decrease.	70.8	12.5	504
OE2	It is important for you to maintain seed dispersal and flower pollination on your farm.	97.4	1.6	504
OB3	If you kill bats, it would be harmful to nature.	79.4	6.7	504
OE3	It is important for you to conserve nature on your farm.	99.4	0.2	504
NB1	Your neighbors would approve of you killing bats.	26.6	50.4	504
MC1	It is important to you what your neighbors think about the management of your farm.	57.3	25.0	504
NB2	Other people who do the same work as you would approve of you killing bats.	24.0	43.3	504
MC2	It is important to you what others who do the same work think about the management of your farm.	67.9	20.4	504
NB3	MINAE would approve of you killing bats.	3.6	9.1	504
MC3	It is important to you what MINAE thinks about the management of your farm.	68.7	19.4	504
NB4	Members of your family would approve of you killing bats.	31.0	19.0	504
MC4	It is important to you what your family members think about the management of your farm.	93.1	3.4	504
NB5	Conservationists would approve of you killing bats.	2.8	9.3	504
MC5	It is important to you what conservationists think about the management of your farm.	77.6	14.5	504

Table 4.5. Pearson covariance matrices for three structural equation models.

(*a*) Direct determinants model

	PC	*OA*	*NP*
BE	0.036	0.465	0.209
BI	0.04	0.637	0.069

(*b*) Outcome attitude model

	OA	*OB1 × OE1*	*OB2 × OE2*	*OB3 × OE3*	*VA*	*NH*
OA	1.238					
OB1 × OE1	2.992	28.417				
OB2 × OE2	-2.282	-2.457	28.572			
OB3 × OE3	-2.91	-7.156	13.407	27.146		
VA	0.171	0.443	-0.455	-0.731	0.207	
NH	-0.438	-1.514	1.45	1.489	-0.083	1.419

(*c*) Normative pressure model

	NP	*NB1 × MC1*	*NB2 × MC2*	*NB4 × MC4*	*NH*	*VA*
NP	0.976					
NB1 × MC1	1.476	16.918				
NB2 × MC2	1.716	8.493	17.145			
NB4 × MC4	2.55	7.241	8.27	22		
NH	-0.249	-0.79	-0.846	-1.031	1.419	
VA	0.118	0.484	0.377	0.563	-0.083	0.207

Table 4.6. Estimated model parameters for structural equation models. Relationship type is abbreviated C = covariance; I = intercept; R = regression; V = variance.

X_1	X_2	Type	Unstandardized coefficient	Standard error	Z	*P*	Standardized coefficient
(*a*) Direct determinants model							
BE	*BI*	R	0.579	0.082	7.021	0.000	0.499
BE	*PC*	R	0.012	0.067	0.184	0.854	0.014
BI	*OA*	R	0.642	0.03	21.452	0.000	0.752
BI	*NP*	R	0.075	0.029	2.589	0.010	0.078
BI	*PC*	R	0.04	0.02	2.026	0.043	0.052
BI	1	I	1.055	0.13	8.086	0.000	1.117
(*b*) Outcome attitude model							
OA	*OB/E1*	R	0.086	0.009	9.866	0.000	0.41
OA	*OB/E2*	R	-0.043	0.009	-4.594	0.000	-0.205
OA	*OB/E3*	R	-0.064	0.01	-6.136	0.000	-0.298
OB/E1	*VA*	R	1.753	0.503	3.483	0.000	0.149
OB/E1	*NH*	R	-0.964	0.196	-4.911	0.000	-0.215
OB/E2	*NH*	R	0.914	0.19	4.818	0.000	0.204
OB/E2	*VA*	R	-1.832	0.508	-3.607	0.000	-0.156
OB/E3	*VA*	R	-3.187	0.497	-6.41	0.000	-0.278
OB/E3	*NH*	R	0.863	0.204	4.218	0.000	0.197
OB/E1	*OB/E2*	C	-0.261	1.415	-0.185	0.854	-0.01
OB/E2	*OB/E3*	C	10.706	1.314	8.149	0.000	0.429
OB/E1	*OB/E3*	C	-4.439	1.33	-3.337	0.001	-0.179
VA	*NH*	C	-0.083	0.026	-3.201	0.001	-0.154
OA	1	I	3.216	0.236	13.649	0.000	2.89
OB/E1	1	I	16.8	0.673	24.966	0.000	3.152
OB/E2	1	I	14.013	0.658	21.289	0.000	2.622

Table 4.6. continued

X_1	X_2	Type	Unstandardized coefficient	Standard error	Z	*P*	Standardized coefficient
OB/E3	1	I	15.831	0.738	21.452	0.000	3.039
VA	1	I	0.292	0.02	14.346	0.000	0.642
NH	1	I	3.032	0.053	56.858	0.000	2.545
OA	*OA*	V	0.7	0.052		0.700	0.565
OB/E1	*OB/E1*	V	26.181	1.444		26.181	0.921
OB/E2	*OB/E2*	V	26.412	1.503		26.412	0.924
OB/E3	*OB/E3*	V	23.533	1.386		23.533	0.867
VA	*VA*	V	0.207	0.008		0.207	1
NH	*NH*	V	1.419	0.078		1.419	1
(*c*) Normative pressure model							
NP	*NB/MC1*	R	0.027	0.012	2.249	0.025	0.111
NP	*NB/MC2*	R	0.043	0.012	3.665	0.000	0.18
NP	*NB/MC4*	R	0.091	0.011	8.383	0.000	0.432
NB/MC1	*NH*	R	-0.43	0.159	-2.696	0.007	-0.124
NB/MC1	*VA*	R	2.166	0.413	5.242	0.000	0.239
NB/MC2	*NH*	R	-0.501	0.157	-3.186	0.001	-0.144
NB/MC2	*VA*	R	1.619	0.405	4.001	0.000	0.178
NB/MC4	*NH*	R	-0.58	0.167	-3.468	0.001	-0.147
NB/MC4	*VA*	R	2.488	0.457	5.441	0.000	0.241
NB/MC1	*NB/MC2*	C	7.314	1.094	6.688	0.000	0.462
NB/MC1	*NB/MC4*	C	5.58	1.251	4.459	0.000	0.317
NB/MC2	*NB/MC4*	C	6.843	1.132	6.046	0.000	0.381
NH	*VA*	C	-0.083	0.026	-3.201	0.001	-0.154
NP	1	I	0.984	0.115	8.589	0.000	0.997
NB/MC1	1	I	11.178	0.543	20.597	0.000	2.718

Table 4.6. continued

X_1	X_2	Type	Unstandardized coefficient	Standard error	*Z*	*P*	Standardized coefficient
NB/MC2	1	I	11.784	0.576	20.463	0.000	2.846
NB/MC4	1	I	12.613	0.596	21.172	0.000	2.689
NH	1	I	3.032	0.053	56.858	0.000	2.545
VA	1	I	0.292	0.02	14.346	0.000	0.642
NP	*NP*	V	0.631	0.046			0.646
NB/MC1	*NB/MC1*	V	15.531	1.273			0.918
NB/MC2	*NB/MC2*	V	16.112	1.234			0.94
NB/MC4	*NB/MC4*	V	20.002	1.541			0.909
NH	*NH*	V	1.419	0.078			1
VA	*VA*	V	0.207	0.008			1

Table 4.7. Total effects of precursor variables, beliefs, and attitudes on attitudes and behavioral intention.

Variable	Standardized	Unstandardized	Standard error	*P*
Total effects on behavioral intention (BI)				
Outcome attitude (*OA*)	0.82	0.70	0.03	<0.001
Normative pressure (*NP*)	0.61	0.53	0.03	<0.001
Perceived behavioral control (*PC*)	0.23	0.20	0.02	<0.001
Total effects on outcome attitude (*OA*)				
Killing roosting bats...				
...reduces livestock damage and disease (*OB1* × *OE1*)	0.51	0.99	0.22	<0.001
...reduces seed dispersal and pollination (*OB2* × *OE2*)	-0.40	-1.54	0.31	<0.001
...damages nature (*OB3* × *OE3*)	-0.52	-1.78	0.30	<0.001
Natural history score (*NH*)	-0.22	-0.21	0.03	<0.001
Vampire problems (*VA*)	0.21	0.45	0.08	<0.001
Total effects on normative pressure (*NP*)				
Would approve of me killing bats...				
...Neighbors (*NB1* × *MC1*)	0.38	1.53	0.25	<0.001
...Others who do the same work (*NB2* × *MC2*)	0.43	1.37	0.22	<0.001
...Family members (*NB4* × *MC4*)	0.56	0.88	0.19	<0.001
Natural history score (*NH*)	-0.13	-0.12	0.02	<0.001
Vampire problems (*VA*)	0.18	0.36	0.06	<0.001

4.6. Discussion

The data indicate that men and women in Coto Brus had predominately negative perceptions of bats. Perceived interactions revolved around bats roosting in houses and damage incurred by the common vampire bat. Whereas most people had some natural history knowledge, very few were able to distinguish among bat species. More than a quarter of rural men in Coto Brus said that if they found a bat roost on their farm they would either kill the bats or burn the roost. This subset of respondents was likely to believe that killing bats would reduce damage to livestock. In contrast, men who said they would leave bat roosts alone were likely to believe that killing bats damages nature and reduces ecosystem services. Respondents with greater natural history knowledge and no personal experience with vampire bats held stronger pro-conservation beliefs than other respondents, and the total effects of environmental education and exposure to vampire bat depredation on planned bat killing behavior were evident in a direct comparison. Collectively, these observations highlight several opportunities for regional bat conservation.

4.6.1. Environmental Education

First, these results support the notion that environmental education is an appropriate tool for improving bat conservation outcomes in Costa Rica (RELCOM 2010). Costa Rican men with greater natural history knowledge were more likely to have a negative attitude about bat killing, and attitude was the most important predictor of bat killing intentions and behavior. Environmental education aims to increase public knowledge about the environment and stimulate motivation to solve environmental problems (Stapp 1970). To do so effectively, Hungerford and Volt (1990) suggest that education should provide relevant ecological knowledge, opportunities to develop environmental sensitivity, in-depth knowledge of environmental issues, problem-analysis and problem-solving skills, and behavioral reinforcement.

I found that a lack of entry-level ecological knowledge was a particularly important limitation on pro-conservation behavior in Coto Brus. Farmers who are unaware of the existence of non-vampire bats, for instance, are unlikely to recognize that burning a bat roost may have negative consequences and will perhaps be more likely to use inappropriate and ineffective pest-control methods, such as baiting fruit bats with poisoned bananas. This conclusion should not dismiss the importance of other educational components, such as providing opportunities for development of environmental sensitivity (Pooley and O'Connor 2000), which may be easier said than done. After a public lecture on bat ecology in Coto Brus, for example, a local woman told me that she now believed that not all bats were vampires, but she still thought that they were ugly and undesirable.

An element of human-bat interactions that was conspicuously absent from my interviews was the array of benefits that bats accrue for humans (reviewed by Kunz et al. 2011). I was particularly surprised that coffee farmers did not have a different view of bats than cattle producers (though most cattle farmers were coffee producers until prices collapsed). Given the importance of bat-mediated insect pest management on coffee plantations, coffee producers should be natural allies of bat conservation (Williams-Guillén et al. 2008). Local men and women discussed the role of bats in increasing disease transmission (*i.e.*, rabies), but no one mentioned insect consumption by bats as a means of reducing the prevalence of mosquito-borne diseases such as dengue (Reiskind and Wund 2009). The lack of recognition of societal benefits from bats suggests that environmental education could improve perceptions of bats by disseminating scientific information that already exists.

An intriguing facet of the human-bat relationship that could also be addressed by environmental education is the persistent impact of the *Dracula* story on human-bat interactions. Early European explorers, naturalists, and taxonomists who visited the Americas created a legacy of misinformation through exaggerated stories of blood-sucking, poor anatomical assumptions (e.g., that the nose leaf of Phyllostomid bats was used to puncture victims), and application of the root *vampyr* to the Latin names of many non-sanguivorous bats – though not any actual vampires (Schutt 2008). More than a century after these misconceptions were reinforced in Bram Stoker's (1897) *Dracula*, some people in Coto Brus continue to use garlic to ward vampires away from their homes and livestock, a method with dubious efficacy for vampire prophylaxis (Jain and Apitz-Castro 1987).

What is the most appropriate audience for bat-related environmental education? Many environmental education programs target children rather than adults, partially in expectation that children's views will influence their parents (Damerell et al. 2013). This could be an effective use of resources in southern Costa Rica where adult men were largely indifferent to the opinions of the Ministry of Environment or conservationists but highly valued the opinions of family members, including children. Additionally, adult men may not be the only demographic that kills roosting bats; two thirds of male survey respondents indicated that they had killed bats when they were young. A current bat education program at Tirimbina Biological Reserve in northern Costa Rica targets multiple audiences by providing repeated programs, first for local school children and later for the same children with their parents and other community members (E. Cordero *pers. comm.* 2011). This iterative approach provides important reinforcement.

In addition to Tirimbina, several other organizations provide bat-related environmental education in Latin America. Since 1982, U.S.-based Bat Conservation International has been educating children, teachers, decision-makers, and the general public about bat biology and conservation (www.batcon.org). This organization also provides start-up grants for environmental education programs in other countries. In 1995, Bat Conservation International helped initiate the Program for the Conservation of Migratory Bats in Mexico and the United States (Walker 1995), which has provided environmental education to targeted communities near high-priority bat caves in Mexico. It has also sponsored teacher training workshops and made educational materials publicly available. Most recently, bat conservationists from 15 countries in Latin America and the Caribbean have formed the Latin American Network for Bat Conservation. This organization has proposed several modes of intervention to stop bat population declines and increase knowledge, appreciation, and respect for bats (RELCOM 2010). These include habitat protection and creation, environmental education, dissemination of bat-friendly pest control methods, and increased research.

Unfortunately, bat-related environmental education efforts rarely reach southern Costa Rica. Instead, the majority of respondents in this study were primarily informed about bats through television. People with exposure only to television scored equally well on a natural history survey compared to people who had participated in more traditional environmental education programs. This result is promising for improving ecological knowledge and pro-conservation behavior across a wide range of remote locations where television and the internet have penetrated more rapidly than progressive social programs (Pearson et al. 2011). The Program for the Conservation of Migratory Bats in Mexico and United States has already begun to take advantage of television as a medium.

4.6.2. Mitigating Vampire-Mediated Risks to Rural Livelihoods

In tandem with natural history knowledge, exposure of respondents to livestock damage incurred by vampire bats was a key predictor of relevant beliefs about killing roosting bats. Given that vampire bat depredation of cattle and chickens was widespread in Coto Brus, conservation efforts that incorporate vampire bat risk mitigation as part of their strategy will likely meet greater success in changing or preventing bat killing behavior.

The fact that vampire bat experience was an important factor for determining outcome attitude, but credit availability, formal education, and relative affluence were not, suggests that risk, but not vulnerability, may be an underlying driver of bat killing behavior. Vulnerability can be defined as the characteristics of an individual's situation that affect his or her capacity to resist, avoid, or cope with loss (Wisner et al. 2003). An individual in Coto Brus might have greater vulnerability to damage by vampire bats if, for example, he lacked access to bank credit (perhaps due to untitled land) and instead kept his savings in cattle (e.g., Dercon 1998, Valdivia 2004) - a strategy that would expose him to greater overall loss than other cattle producers in the event of a rabies epidemic, for example. Risk, in contrast, refers to consequential livelihood uncertainty (Winterhalder et al. 1999). Intermittent vampire bat damage to livestock represents a risk for many cattle producers in Coto Brus, and it is likely contingent on situational factors such as the density of food and roosting resources in the surrounding landscape (Gomes et al. 2010) and whether or not an individual has experienced vampire attacks in the past. My results suggest that several possible measures of vulnerability (affluence, credit access, education) were less important for predicting bat-killing beliefs than previous vampire bat experience - a measure that likely correlates with risk of future vampire bat attacks.

Why should individuals with differing levels of vulnerability take equal measures to reduce risk? One explanation may be that the perceived cost of risk reduction is low, so that any individual with any risk is better off trying to reduce it. During my interviews, most informants felt that killing roosting bats would not be difficult, and no informant ever expressed the opinion that killing bats might be illegal. Indeed, it is not. Costa Rica's wildlife law is based on the Convention on International Trade of Endangered Species (CITES; 1973, 1992), and CITES does not list any Costa Rican bats as endangered (UNEP-WCMC 2010). Additionally, the Ministry of the Environment and general law enforcement in Costa Rica are often seen as ineffective (Salazar 2004), so killing roosting bats can be done with impunity.

I also found evidence that respondents who kill bats may not have sufficient information to recognize the costs associated with their actions. Whereas many farmers in southern Costa Rica are likely to benefit from the services provided by bats, my interviews suggest that a farmer who makes an initial investment in a container of Warfarin poison is approximately equally likely to use it as recommended by applying it to a wound site on a cow (a rational action) or spread it on a banana or in a container of sugar water, likely killing fruit and nectar bats without harming any vampires (an irrational action). Whereas killing vampire bats probably represents a risk-averse behavior, smallholders may actually increase their risk of mosquito-borne disease or reduced crop growth by killing beneficial insectivores. Livelihood studies in Kenya and in central Costa Rica have similarly found that smallholders will sometimes minimize short-term risk when long-term consequences are unrecognized (Mannon 2005). It should be noted that vampire bats may also benefit rural farmers by redistributing limiting nutrients such as nitrogen and phosphorus (Emerson and Roark 2007) and through medicines based upon an anticoagulant in their saliva (Bang 1991).

Importantly, livelihood risks are highly subjective (Ellis 1988). It is well documented that common vampire bats feed predominantly on livestock, and many bat biologists concur that vampire populations have probably increased since European colonization and the introduction of cattle (LaVal 2004, Voigt and Kelm 2006). Yet some bat biologists disagree with the practice of culling vampire bats and do not consider vampire bats a serious threat to cattle production in Costa Rica. I argue that the magnitude of the realistic threat of vampire bats to agriculture is not important as long as the risk that farmers perceive is sufficiently great for them to justify roost destruction even when the species composition of roosting bats is unknown to them.

4.6.3. An Opportunity for Bat Conservation

If the primary barriers to bat roost conservation in Coto Brus are a lack of ecological knowledge and widespread livelihood risk associated with vampire bats, then a conservation strategy combining these elements may be useful. One approach could be to engage and educate adult cattle producers by capturing bats and lethally controlling vampires on their farms. Beneficial bats, such as frugivores, nectarivores, and insectivores, could be shown to farmers and then released, and vampire bats could have Warfarin applied to their dorsum and then be released. When Warfarin-treated vampire bats return to their colonies, multiple individuals may be killed via social grooming of the treated individual (Greenhall 1974). This method is described in a Spanish-language video produced by Bat Conservation International (Walker 2002). It is safer and more effective for controlling vampire bats than a simple application of Warfarin around a vampire-induced laceration on a cow, and when properly conducted it does not affect non-vampire species. It also gives adult farmers a hands-on educational experience and allows them to learn about the characteristics that distinguish vampire bats from other species - information that was nearly absent from my study population.

Such an approach would require trained technicians to carry out the work in order to prevent misidentification of bat species and minimize risk to individuals handling bats. The Ministry of Agriculture formerly offered a targeted vampire bat control service in Coto Brus but no longer does. For similar production-specific problems in coffee, local cooperatives have often provided technical assistance (Sick 1999), but no such institutions seem to exist for cattle producers in southern Costa Rica. Ideally, local people could be trained to educate farmers and safely control vampire bat populations. Bat conservation efforts elsewhere have been more successful when they incorporated local educators (Trewhella et al. 2005). Such efforts will also be more successful if coordinated at a regional scale (Streicker et al. 2012).

4.6.4. Conclusions

Predicting human behavior is critical for effectively addressing a variety of conservation problems. I found that the theory of reasoned action was a practical and informative approach for identifying barriers and opportunities for bat conservation in southern Costa Rica, and I anticipate that it could provide insights for a variety of other conservation problems. In essence, the theory purports that human behavior is guided by considerations of a behavior's consequences, social pressures, and perceived ease or difficulty. Evaluation of the relative importance of these three components permits the formulation of pointed interventions to reinforce positive beliefs held by individuals, and help change negative beliefs.

I used a conservation psychology approach to demonstrate the range of perceptions, knowledge, and human-bat interactions in Coto Brus County and to identify barriers and opportunities for conserving local bat populations. Killing of roosting bats is an important conservation concern throughout Latin America, and Coto Brus is no exception. Natural history knowledge and exposure to vampire bat depredation of livestock were key predictors of beliefs relating to the killing of roosting bats. Based on these results, I suggest that an integrated conservation effort including education about bat biology and effective control of vampire bat populations could be an effective intervention to support pro-conservation behavior. Whereas this study took place over a relatively small area, the main actors (humans, bats, cattle, and coffee) are widespread throughout Latin America, and many of these conclusions may apply in a variety of rural settings where farmers underestimate the value of beneficial bats and have some livelihood risk associated with damage by the common vampire bat.

4.7. Acknowledgements

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5. Appendices

Appendix 1. Conservation prompts for focus group interviews

Introducción

¡Gracias por venir hoy para compartir sus ideas sobre animales con nosotros! Mi nombre es Karolina, y el compañero que está grabando la entrevista es Leighton. Este grupo de enfoque va a tomar no más que dos horas, y después vamos a tener un refrigerio. Ustedes ya han recibido información sobre sus derechos como participantes en el estudio. Antes de empezar, quiero recordarles que deseamos oír las opiniones de todos los participantes. Entonces no hay razón de estar tímido. También, si alguien esta dominando la conversación, voy a solicitar suavemente las opiniones de otros miembros del grupo. En todo, recuerdan que lo más importante es tener respeto para otros participantes.

¡Bueno – tenemos un grupo excelente y yo creo que vamos a tener una conversación libre y divertida! Pienso que estamos listos.

Pregunta de Empezar

(1) Para empezar ¿Quién es usted, donde vive, y en que trabaja?

Pregunta de Introducción

(2) Para empezar, aquí es una foto de un animal. ¿Cuando usted vea esta foto, que palabras vienen a su mente? ****Participants were shown an illustration of* Carollia

perspicillata *from Fiona Reid's (2009) A Field Guide to the Mammals of Central American and Southeast Mexico (Oxford University Press, New York, New York).*

Preguntas Transitorias

(3) Recuerda haber tenido una experiencia memorable con murciélagos. ¿Cómo fue la experiencia?

(4) Describa su idea de que es un murciélago.

Preguntas Claves

(5) ¿Que ha oído usted sobre murciélagos?

(6) ¿Qué le gustaría saber sobre murciélagos?

(7) ¿Cómo afectan los murciélagos a su vida? *¿Su trabajo? ¿La Agricultura? ¿Algo positivo? (si la conversación va negativo demasiado rápido)*

Después de que alguien dice algo negativo como un problema que causan los murciélagos: (8) ¿Que pueden hacer la gente para prevenir este/estas problema(s)?

Preguntas Finales

(8) ¿Que otros opiniones tiene usted que no ha tenido oportunidad de compartir?

(9) ¿Que más debemos preguntar que no preguntamos?

Conclusión

Ya hemos llegado al fin de este grupo de enfoque. La información que han compartido va a ayudar esfuerzos de manejo responsable de recursos naturales. En unos dos años a la terminación del proyecto, los resultados serán compartidos en unas charlas y con folletos. Muchísimas gracias por su participación, y pueden encontrar los refrigerios….[donde están…

Appendix 2. Questions from Natural History Survey

1. [Informant is shown an illustration of *Carollia perspicillata*] ¿Cómo se llama este animal?

2. [Participant is shown 10 flashcards depicting various local bat species and one non-native species*] ¿Cuáles de estos ha visto usted aquí en la comunidad?

3. ¿Qué tipos de comida comen estés animales?

4. [Informant is shown all 10 flashcards] ¿Cuál de estos es un vampiro?

*Flashcards included illustrations of *Artibeus literatus*, *Carollia perspicillata*, *Centurio senex*, *Desmodus rotundus*, *Glossophaga soricina*, *Micronycteris microtis*, *Sturnia ludovici* (Phyllostomidae), *Myotis keaysi* (Vespertilionidae), *Saccopteryx bilineata* (Emballonuridae), and *Hipposideros diadema* (Hipposideridae).

Appendix 3. Pilot survey administered to 30 men in November-December 2011.

Día ___________ Mes__________ Año _____________ Hora de inicio_______________

Distrito ____

****

Introducción. La Universidad de California está dirigiendo un estudio para determinar la relación entre seres humanos y murciélagos. Estamos entrevistando muchas personas en Coto Brus acerca de sus opiniones sobre murciélagos, nos gustaría contar con su participación. La entrevista tardará cerca de 15 minutes, no existen respuestas correctas o equivocadas. La información que usted nos suministre será confidencial y su nombre no aparecerá en ningún reporte como resultado del estudio. Su participación es voluntaria, si en algún momento no desea responder una pregunta, no tiene por qué hacerlo. ¿Podemos iniciar la entrevista?

****

1. Para iniciar, qué edad tiene? _______ años

SI ES MENOR DE EDAD FINALICE LA ENTREVISTA

****

2. Imagine que mañana usted esta caminando en su finca y encuentra un árbol con un hoyo con murciélagos durmiendo en su interior. Usted no puede verlos bien pero usted puede decir que al menos hay 10 durmiendo ahí dentro. ¿Qué haría usted? recuerde que no hay respuestas buenas o malas solo estamos interesados en su opinión.

____
____
____
____
____

3. Muchas personas dicen que si encuentran un nido murciélagos en su finca ellos lo destruirán. Si usted destruyera un nido de murciélagos en su finca ¿cuales serian las ventajas para usted?

   a. ____
   ____

   b. ____
   ____

   c. ____
   ____

   d. ____
   ____

   e. ____
   ____

4. ¿Cuales serian las desventajas de destruir los nidos de murciégalos de su finca?

   a. ____
   ____

   b. ____
   ____

   c. ____
   ____

   d. ____
   ____

   e. ____
   ____

5. Por favor enliste las personas o grupos que aprobarían que usted destruya los nidos de murciélagos en su finca.

   a. ____
   b. ____
   c. ____
   d. ____
   e. ____

6. Por favor enliste las personas o grupos que desaprobarían que usted destruya los nidos de murciélagos de su finca.

   a. ____
   b. ____
   c. ____
   d. ____
   e. ____

7. Quien es la persona con la que usted trata de quedar bien cuando toma decisiones acerca de su finca

   a. ____
   b. ____

c. ____

d. ____

e. ____

8. ¿Que haría para usted difícil destruir un nido murciélagos de su finca?

a. ____

b. ____

c. ____

d. ____

e. ____

9. ¿Que haría para usted fácil destruir un nido de murciélagos de su finca?

a. ____

b. ____

c. ____

d. ____

e. ____

10. Hay algo mas que usted considera importante tener en mente cuando decide o no decide destruir un nido de murciélagos.

____
____
____
____
____

Aquí concluye nuestra entrevista. Muchas gracias por su participación.

****

Impresiones del entrevistador

Hora en que finaliza _____________________________________

De qué manera se entendieron las preguntas

Muchos problemas (1)

Algunos problemas (2)

Sin problemas (3)

Otros comentarios

____
____
____
____

Appendix 4. Large survey administered to 500 men in Coto Brus in Jan-Mar 2012.

MES____ DIA____ HORA INICIO_________ DISTRITO: AB GU LI PI SB SV COMUNIDAD______________________

Introducción. La Universidad de California está realizando un estudio sobre murciélagos y su relación con los hogares y familias. Para esto, estamos entrevistando algunas personas del cantón de Coto Brus solicitando su valiosa colaboración. La información que usted nos dará será confidencial. Su nombre no aparecerá en ningún documento como resultado del estudio. Su participación es voluntaria, si usted desea no contestar una pregunta o terminar la entrevista podrá hacerlo cuando desee. La participación en esta encuesta no representa ningún riesgo. La encuesta tardara alrededor de 15 minutos y de nuevo, su participación es totalmente voluntaria. Al final daremos información sobre murciélagos en la Zona Sur. ¿Podemos iniciar la encuesta?

1.	¿Qué edad tiene usted?	Años **(HAY QUE TENER >18)**
2.	¿A qué grupo pertenecen los murciélagos?	AVES MAMIFEROS REPTILES NO SABE
3.	¿Qué comen los murciélagos cuando nacen?	INSECTOS SANGRE LECHE NO SABE
4.	¿Cuántos dedos tienen los murciélagos?	3 5 NO TIENEN NO SABE
5.	¿Qué animal se come a los murciélagos?	LECHUZA JAGUAR COCODRILO NO SABE
6.	¿Todos los murciélagos son vampiros que chupan sangre?	SI NO NO SABE

7. Si Ud. esta caminando en su finca y encuentra un árbol que tiene un hueco con murciélagos durmiendo a dentro, ¿Qué haría usted?

NO LEER OPCIONES NADA MATARLOS PRENDER FUEGO ESPANTARLOS OTRO________________________

Voy a leer algunas opciones de lo que pasaría si usted encontrara murciélagos durmiendo en el hueco del árbol en su finca. Por favor indique si usted está de acuerdo, en desacuerdo, o neutral.
(RECUERDA QUE ES SOLAMENTE PARA LA SITUACION EN QUE ENCUENTRA MURCIELAGOS EN UN HUECO DE ARBOL)

		Desacuerdo mucho	Desacuerdo	Neutral	Acuerdo	Acuerdo mucho
8.	Ud. tiene la capacidad de matar murciélagos si tiene que hacerlo.	1	2	3	4	5
9.	La mayoría de las personas cuyas opiniones son importantes para Ud. aprobarían que usted mata a los murciélagos si los encuentra en un árbol en la finca.	1	2	3	4	5
10.	Si Ud. encuentra murciélagos, lo mejor para Ud. seria matarlos.	1	2	3	4	5
11.	Sus vecinos aprobarían que Ud. mata los murciélagos.	1	2	3	4	5
12.	Otras personas que hacen el mismo trabajo que Ud. aprobarían que Ud. mata los murciélagos.	1	2	3	4	5
13.	El MINAE aprobaría que Ud. mata los murciélagos.	1	2	3	4	5
14.	Miembros de su familia aprobarían que Ud. mata los murciélagos.	1	2	3	4	5

15.	Los conservacionistas aprobarían que Ud. mata los murciélagos.	1	2	3	4	5
16.	Es importante para Ud. a mantener la salud de las vacas y animales domésticos.	1	2	3	4	5
17.	Es importante para Ud. a mantener la dispersión de semillas y polinización de flores en la finca	1	2	3	4	5
18.	Es importante para Ud. a cuidar la naturaleza en la finca.	1	2	3	4	5
19.	Si Ud. encuentra murciélagos durmiendo en un hueco de árbol en la finca, Ud. los va a matar.	1	2	3	4	5
20.	Es importante para Ud. lo que piensan otras personas que hacen el mismo trabajo que Ud. sobre el manejo de la finca.	1	2	3	4	5
21.	Es importante para Ud. lo que piensa el MINAE sobre el manejo de la finca.	1	2	3	4	5
22.	Es importante para Ud. lo que piensan los conservacionistas sobre el manejo de la finca.	1	2	3	4	5
23.	Es importante para Ud. lo que piensan los miembros de su familia sobre el manejo de la finca.	1	2	3	4	5
24.	Es importante para Ud. lo que piensan sus vecinos sobre el manejo de la finca.	1	2	3	4	5
25.	La única opinión que cuenta cuando Ud. toma decisiones sobre el manejo de la finca es la suya.	1	2	3	4	5
26.	Si Ud. mata los murciélagos, la dispersión de semillas y polinización de flores en la finca podrían bajar.	1	2	3	4	5
27.	Si Ud. mata los murciélagos, podría prevenir daño y enfermedades a las vacas u otros animales.	1	2	3	4	5
28.	Si Ud. mata los murciélagos, sería un daño a la naturaleza.	1	2	3	4	5

29.	¿Tiene Ud. esposa? **(NO → IR A 32)**		NO	SI		
30.	La esposa aprobaría si Ud. mata los murciélagos.	1	2	3	4	5
31.	Es importante a Ud. lo que piensa la esposa sobre el manejo de la finca.	1	2	3	4	5

32.	¿Trabaja usted para un patrón en la finca? **(NO → IR A 35)**		NO	SI		
33.	El patrón aprobaría que Ud. mata los murciélagos.	1	2	3	4	5
34.	Es importante a Ud. lo que piensa el patrón sobre el manejo de la finca.	1	2	3	4	5

35.	¿Tiene Ud. hijos entre las edades de 5-18 años? **(NO → IR A 39)**		NO	SI		
36.	Los hijos aprobarían que Ud. mata los murciélagos.	1	2	3	4	5
37.	Es importante a Ud. lo que piensan los hijos sobre el manejo de mi finca.	1	2	3	4	5
38.	Si los hijos encuentran murciélagos en un hueco de árbol, los van a matar.	1	2	3	4	5

39.	En los últimos 5 años ¿Cuántos murciélagos cree que usted ha matado en sus nidos?				murci.	
40.	¿Cuando Ud. era niño, mato Ud. murciélagos de una vez?		NO	SI		

41. ¿Cuál es el nivel más alto de estudio que Ud. ha completado?

NINGUNO
GRADO ESCUELA 1 2 3 4 5 6

GRADO COLEGIO 1 2 3 4 5 6
NIVEL UNIVERSITARIO 1 2 3 4 5 6+

42. ¿Ha estado Ud. en una presentación sobre educación ambiental? SI NO
    a. ¿Tenía esta presentación información sobre los murciélagos? SI NO
43. ¿Ha Ud. visto programas de televisión sobre murciélagos? SI NO

Ya casi terminamos. Voy a preguntarle sobre sus finanzas personales. Si no quiere contestar, no tiene que hacerlo, pero esta información ayudaría mucho al proyecto. Solamente vamos a usar esta información para esta investigación, y la información que usted nos dé no estaría asociada con su nombre.

44. ¿Tiene Ud. crédito en un banco? SI NO

45. Por favor, podría estimar los ingresos totales de su hogar en el año 2011. La estimación debe incluir todo lo que la familia ganó el año pasado, y no solamente lo que ganó con una cosa o la otra. (No tiene que ser exacto. Estamos usando una escala de rangos)(en colones).

<500.000 colones
500.000-1.000.000 colones
1.000.000-1.500.000 colones
2.000.000-3.000.000 colones
3.000.000-5.000.000 colones
>5.000.000 colones

46. ¿Trabaja Ud. en una finca? SI NO **(NO → IR A 47)**
    a. ¿Cuántas hectáreas tiene la finca? ________________ hectáreas
    b. ¿Qué produce esa finca?

    CAFÉ GANADO POLLO TOMATE OTROS__________________

    c. **CAFÉ:** ¿Cuantas hectáreas están sembrado en café? ___________________________hectáreas
    d. **GANADO:** ¿Cuántsos ganado están en la finca? ___________________________ganado
    e. ¿Ha tenido Ud. problemas con vampiros atacando a los ganado? SI NO
    f. **POLLO:** ¿Cuántos pollos están en la finca? ____________________________pollo
    g. ¿Ha tenido Ud. problemas con vampiros atacando a los pollos? SI NO

47. ¿Qué fue la primera idioma que Ud. aprendió?

(**NO LEER OPCIONES**) ESPANOL NGÄBERE OTRO___________________

48. ¿Qué idioma habla su familia en la casa?

(**NO LEER OPCIONES**) ESPANOL NGÄBERE OTRO___________________

FIN DE LA ENCUESTA. MUCHISIMAS GRACIAS POR PARTICIPAR. PASE LA INFORMACION.

Hora de Finalización:______________ ¿Entendió? 1 2 3 4 5

Latino Indígena Norteamericano Italiano otro__________________ Vivienda 1 2 3 4 5

6. Supplementary files

Video 3.1. *Carollia* species visiting a forest roost during the night.

Video 3.2. *Glossophaga* species visiting a roost in an abandoned pasture during the night.

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