AVIAN BIODIVERSITY AND REDUCED IMPACT LOGGING:

BIRD COMMUNITIES, FOREST STRUCTURE AND ANTHROPOGENIC DISTURBANCE IN A REDUCED-IMPACT LOGGED BOLIVIAN FORESTRY CONCESSION

Chestnut-eared araçari (*Pteroglossus castanotis*) Photo by Annika Felton

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"Epithet after epithet was found too weak to convey to those who have not visited the intertropical regions, the sensation of delight which the mind experiences.....The land is one great wild, untidy, luxuriant hothouse, made by Nature for herself."

Charles Darwin, 1845. The Voyage of the Beagle.

DECLARATION

This thesis is my own work except where otherwise acknowledged (see Acknowledgements and Preface).

Adam Felton
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PREFACE

With the exception of Chapter 1 (Introduction) and Chapter 7 (Conclusion), this thesis consists of a series of interrelated manuscripts. These manuscripts are published, accepted for publication, or submitted for publication. Each manuscript is presented as it appears, or will appear, in the relevant journal with the exception of minor changes in style and formatting. The vast majority of the work that contributed to this thesis was carried out by the primary author (AF), including literature searches, experimental design, data collection, data analysis, and manuscript write-up. However, co-authors are included on each manuscript, acknowledging their contributions to each particular aspect of the research. David Lindenmayer contributed to the overall experimental design, provided important guidance regarding the organization of the research, made important contributions to each paper, and proof-read all manuscripts. Annika Felton contributed in terms of formulating ideas, project design, logistical support, data collection, and proof reading through all stages of the project. Jeff Wood was involved in chapters 2, 3, 4, and 5. He provided statistical advice regarding the appropriate data analysis to use, interpretation of results, and wrote scripts for statistical analysis using the program R where necessary. Bennett Hennessey was involved in chapters 4, 5, and 6. Bennett is one of the World’s few experts of Bolivian bird song and his advice enabled a far higher percentage of the bird fauna to be identified than would otherwise have been possible.

Because the primary chapters of this thesis are manuscripts developed for independent publication in scientific journals, some repetition between chapters was unavoidable.

ABSTRACT

Reducing the damage caused by the commercial selective logging of tropical forests worldwide, and more specifically in the species-rich tropical forests of Latin America, is a global conservation priority. Reduced-impact logging was developed, in part, to minimize the negative impacts of logging on biodiversity. Reduced-impact logging incorporates a variety of techniques aimed at lowering levels of harvesting damage to the residual stand. These techniques include directional felling, pre-harvest vine cutting, and preliminary inventories to reduce the number and density of logging roads. This thesis aimed to contribute to our understanding of the effects of reduced impact logging on biodiversity conservation.

I conducted empirical investigations within Bolivia, in the lowland subtropical humid forest of the Guarayos Forest Reserve, Departmento Santa Cruz. Research was conducted in the 100,000 hectare forestry concession “La Chonta”. Approximately 2 500 ha is harvested annually over three contiguous 850 ha blocks, yielding 50,000 cubic meters of timber product. Average harvest intensity was approximately 4 trees/ha and took place between one and four years prior to this study. A stratified-random sampling design was used to select sites in both harvested and unharvested forest blocks. The strata included commercial tree species occurrence, vegetation height, and disturbance type. This design accounted for natural variation in vegetation structure and increased the likelihood that logged and unlogged survey points were appropriate for comparison.

I assessed the degree to which reduced-impact logging disturbance processes were diverging from natural disturbance processes. To do so I studied differences in gap size, vegetation structure, regeneration and phenology between anthropogenic and natural gaps in the harvested and unharvested areas of the concession (Chapter 2). Logging gaps were significantly larger than natural gaps (df 1, vr. 6.38, $p=0.014$) and had significantly lower coverage of lianas (df 1, vr. 8.64, $p<0.01$). Seedlings were more prevalent in logging gaps than in natural tree fall gaps (df 1, vr. 13.97, $p<0.001$), as were members of the herbaceous genus *Heliconia* (df 4, vr. 3.05, $p=0.023$). In larger gaps microclimatic conditions favoured the regeneration of non-

commercial pioneer species. I propose that ground disturbance during bole removal causes higher rates of mortality to shade-tolerant species in advanced stages of regeneration. This removes the competitive height advantage needed by shade-tolerant species to compete within gaps, and thus further promotes the opportunity for pioneer species to dominate gap regeneration. These observed differences between anthropogenic and natural tree-fall gaps are of direct importance to forest managers attempting to understand how disturbance associated with reduced-impact logging influences the regeneration of commercial tree species in Bolivian forestry concessions.

I examined understorey regeneration within the residual stand and unlogged areas of the concession (Chapter 3). Overall, the unlogged forest and the residual stand of the harvested forest were similar in terms of floristic composition. However, there was a significant difference in vegetation structure and phenology between the unlogged forest and the residual stand retained within the logged forest four years after harvesting ($t=-2.34$, $P<0.05$). The residual stand of the RIL forest had a significantly higher percentage cover of seedlings ($t=2.48$, $P=0.014$) and palms ($t=2.33$, $P=0.021$) than their unlogged counterparts. In contrast the percentage cover of ferns ($t=-2.49$, $P=0.014$) and the number of plants in flower ($t=-2.13$, $P=0.034$) was significantly lower in the understorey of the residual stand four years following harvesting. Results indicate that understorey vegetation in the residual stand may be proceeding along a different successional trajectory from that found within the unlogged forest. As the majority of the residual stand was left undamaged by logging, even subtle changes in the relative dominance of regenerating vegetation over these extensive areas could significantly alter what are considered to be sustainable harvesting intensities. I see these results and accompanying explanatory hypotheses as preliminary, and suggest that assessment of the understorey vegetation structure and phenology of the residual stand is an important area for future research within tropical RIL forestry concessions.

As bird assemblages are strongly influenced by vegetation structure, I determined whether differences were occurring in bird community composition and abundance between the harvested and unharvested areas of the concession (Chapter 5). During point count surveys, I identified over 5 050 birds, belonging to 155 species, and 33 families (Chapter 4). I also assessed whether there was any pattern of sensitivity among different bird families (Chapter 5). I used canonical correspondence analysis

to describe the relationship between selected environmental variables and bird species abundance data, and the Indicator Value procedure to test for associations between bird species and the logged and unlogged habitats. Approximately one-third of birds were restricted to either the logged or unlogged areas, with twenty percent of all species only encountered in, or significantly more abundant in, the unlogged areas of the concession. The majority of birds found in significantly higher abundance in the unlogged areas of the concession were associated with forest habitats dominated by large trees, or a high diversity of trees, providing dense canopy cover and deep leaf litter, with an understorey dominated by ferns. Over forty percent of bird species that were significantly associated with the unlogged areas of the concession are of conservation concern. In contrast, the majority of birds associated with the logged areas of the concession are known to be relatively resilient to human disturbance. The majority of species which exhibited significant lower abundances in the logged areas of the concession belonged to insectivorous or frugivorous feeding guilds. I discuss whether current management practices within this certified concession are sustainable and how our results can be used to guide future research and inform better practice.

After establishing an overall difference in bird community composition between the unlogged and logged areas of the concession, I used correspondence analysis to determine whether bird species composition and abundance could be used to distinguish between vegetation categories within the logged and unlogged forest (Chapter 6). The bird community composition of logging gaps significantly differed from that found within natural tree-fall gaps in the unlogged forest ($p<0.05$). No significant difference was detected in the bird community composition for the other three vegetation categories surveyed.

Four general conclusions arise from this thesis:

1. Anthropogenic disturbance associated with reduced-impact logging has the potential to alter understorey regeneration in areas of the residual stand not directly disturbed by logging activities.
2. Gaps in the canopy caused by reduced-impact logging are not the anthropogenic equivalent of natural-tree fall gaps in terms of regeneration or bird community composition.

3. Reduced-impact logging concessions can maintain a large component of avian biodiversity, but a potentially vital assemblage of bird species appear to be sensitive to associated disturbance processes.
4. The adoption of RIL techniques should be seen as a step towards ecologically sustainable extraction techniques, rather than the obtainment of this goal.

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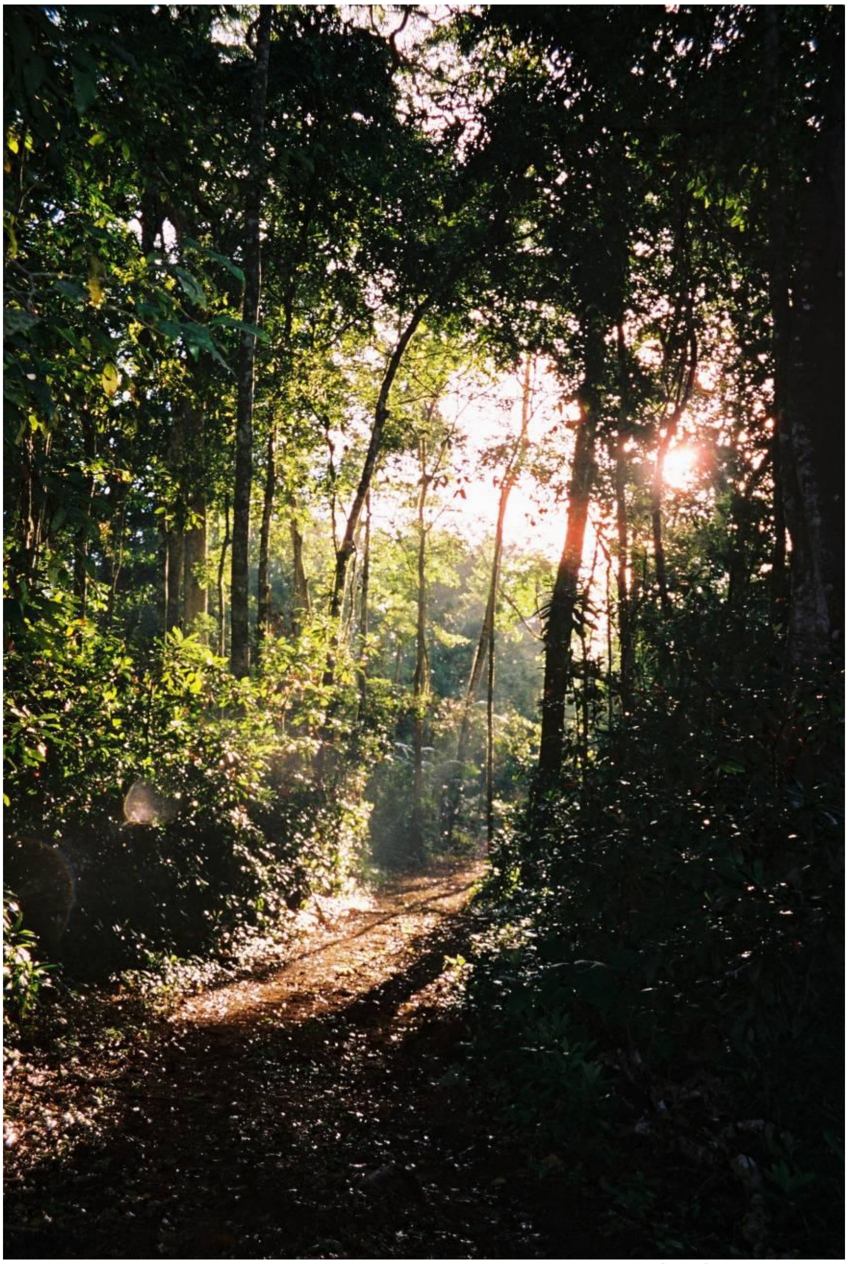

Photo by Petter König

Skid trail entrance leading to our research camp, in the La Chonta forestry concession.

Chapter 1

INTRODUCTION

1.1. Background

Due to accelerating rates of global biodiversity loss, attempts are being made to focus conservation actions on those ecosystems under greatest threat and possessing a disproportionate share of the world's biodiversity (Myers et al., 2000; Sala et al., 2000). Up to two-thirds of the world's terrestrial species are found in tropical forests (Groombridge & Jenkins 2002). Fifteen million hectares of these megadiverse ecosystems are being degraded annually by logging, agriculture, and other anthropogenic disturbances ((FAO) 2001). Therefore, preservation of tropical forest ecosystems will be an integral component of successful global conservation efforts. As insufficient area of tropical forest can be included in protected areas to halt loss of biodiversity (Soulé & Sanjayan 1998), conservation efforts have shifted towards the adoption of land-uses considered compatible with the maintenance of forest biodiversity (Frumhoff & Losos 1998; Putz et al., 2001).

Selective logging is the dominant form of timber extraction in the tropics, and is considered to be one of the land-uses that can potentially reconcile human demands for resources with the need to maintain biodiversity (Rametsteiner & Simula 2003). Selective logging involves the periodic extraction of commercially valuable tree species from forests (Johns 1988b). The largest remaining tracts of tropical forest occur in Latin America (FAO, 2001), and by the mid-1990s an estimated 28% of these forests had been subjected to selective logging (Grieser-Johns, 1997). The extent to which selective logging degrades forest structure varies considerably depending on extraction rates and the extent of collateral damage to the residual stand (Johns 1988b). As a silvicultural system, selective logging therefore represents a continuum of anthropogenic disturbance, which at one extreme may be virtually synonymous with deforestation, and at the other extreme may allow for the retention of much of a forest's original canopy and vegetation structure (van Soest 1998). It is expected that somewhere along this continuum, selective logging practices can be developed that successfully combine economically viable levels of timber extraction with biodiversity conservation (Pinard & Putz 1996a).

Reduced-impact logging (RIL) is a modified form of selective logging that is increasingly employed in tropical forests. It incorporates a variety of techniques aimed at lowering levels of damage to the residual stand (Putz et al., 2001). These include directional felling, pre-harvest vine cutting, and preliminary inventories to reduce the number and density of logging roads (Heinrich 1995). Recent studies suggest that reduced-impact logging of tropical forests causes less damage to forest structure than conventional selective logging techniques (Asner et al., 2004a; Huth et al., 2004). RIL is applied widely in Bolivia and, as of 2005, concessions covering over 2.2 million hectares had obtained certification by the Forest Stewardship Council (FSC, 2005). Underlying this adoption of FSC certification is an expectation that the use of RIL will circumvent many of the ecological problems associated with conventional selective logging practices employed in these regions.

This expectation that RIL techniques will have negligible impacts on forest dependent biota is consistent with statements made by some of the principle certification agencies and conservation NGOs that advocate the adoption of RIL techniques. The FSC has a set of principles and criteria that apply to all forestry concessions which receive their stamp of approval. The FSC's sixth principle is; "Forest management shall conserve biological diversity and its associated values, water resources, soils, and unique and fragile ecosystems and landscapes, and, by so doing, maintain the ecological functions and the integrity of the forest" (FSC, 2006). WWF "considers the Forest Stewardship Council (FSC) certification system to be the only credible system to ensure environmentally responsible, socially beneficial and economically viable management of forests. WWF therefore recommends the FSC system to consumers, forest managers, policy makers, businesses and the public" (WWF, 2006). Furthermore WWF helps to finance the "training of forestry staff in reduced impact logging practices" (WWF, 2006).

This level of endorsement, and the rate at which RIL is being adopted in the tropical world, requires that we have the best possible scientific information regarding the compatibility of RIL with biodiversity maintenance. Discrepancy between the expectations of advocates with what is achievable with current RIL practices could have negative repercussions if: 1) unrealistic views enable selective logging to enter fragile and biodiverse ecosystems where logging should be excluded; or if 2) unrealistic views regarding the conservation value of forests subjected to RIL propulgates a false sense of security regarding current rates of biodiversity loss from large areas of tropical forest. Despite the need for sufficient information to be able address these concerns, little is known about the capacity of forests subjected to RIL to retain their original compliment of biodiversity (Bojanic & Bulte 2002; Dauber et al., 2005).

Ideally, assessments of forest biodiversity responses to RIL would be conducted using landscape-scale controlled and replicated experiments, with decades of results quantifying the responses of forest biota to multiple harvest cycles. Predictably, considering the recent nature of widespread adoption of RIL techniques, together with the rarity of large scale experiments in ecology, such ideals are currently unattainable. Nevertheless, through the use of “natural experiments” (Lindenmayer et al., 2001), as can found within tropical forestry concessions employing RIL techniques, and careful sampling design, important insights can be gained regarding how forest dependent biota are responding over the short term to reduced-impact logging.

1.2. Objective and aims

1.2.1 Objective one

Birds are useful taxon for assessing the impacts of logging on biodiversity in tropical forests. This is because bird community composition can be strongly influenced by disturbance to forest vegetation structure (Wiens 1992; Mason & Thiollay 2001). Studies of conventional selective logging suggest that disturbance to vegetation structure and microclimate affects bird species in a variety of ways, and is highly dependent on the guild being considered (Mason 1996). Each species may react differently to a given forest disturbance depending (in part) on its foraging behavior, habitat specialization, and physiological sensitivity to microclimatic changes (Thiollay 1992). For these reasons, studies of bird species’ responses to tropical forest disturbance have reported negative or positive impacts depending on the extent of disturbance, and the species pool being considered (Hill & Hamer 2004).

My first objective for this thesis was:

- To assess the compatibility of RIL with the maintenance of forest dependent bird communities.

Specifically, I aimed to determine the extent to which bird communities of the harvested and unharvested areas of the concession were distinct in terms of species composition and abundance. I also examined why some taxonomic groups may be sensitive to the conditions produced by RIL, and addressed what may be done to ameliorate the apparent decline of some species.

To satisfy this first objective, I conducted my research in the lowland subtropical humid forest (Holdridge Life Zone System) of the Guarayos Forest Reserve, Departmento Santa Cruz, Bolivia. Research was conducted in the 100,000 hectare forestry concession “La Chonta”, owned and managed by Agroindustria Forestal La Chonta (509000 to 545000 easting, 8275500 to 824900 northing; Appendix 2). I used a stratified-random sampling design to select sampling sites in both harvested and unharvested forest blocks. Point count surveys to gather bird species composition and abundance data were conducted within 360 sampling sites within the harvested and unharvested areas of the concession. These sites were randomly located in five different strata based on commercial tree species occurrence, vegetation height, and disturbance type.

The maintenance of avian species diversity is of concern to both conservationists and forest managers. First, quantitative assessment of the IUCN red list shows that the threat status of the world’s birds has steadily worsened since 1988 (Butchart et al., 2004), with 93% of threatened forest avifauna found in tropical forests (Birdlife-International 2004). Second, in addition to their intrinsic value, birds perform vital ecological functions in tropical forests, through their roles as pollinators, seed dispersers, scavengers, ecosystem engineers, and predators (Stiles 1983)). Changes to the composition of bird communities may have negative repercussions for forest ecology if those species which decline or are eradicated performed ecological roles not readily filled by disturbance-adapted generalist species.

1.2.2 Objective two

The adoption of RIL procedures does not necessarily equate with the achievement of sustainable levels of extraction, although these techniques can certainly contribute to such a goal. Unfortunately, within the La Chonta concession, the dominance of non-commercial pioneer species in logging gaps (Park et al., 2005), lack of adequate regeneration for most commercial trees (Pariona et al., 2003), and current projections of dramatic declines in the volume of future harvests (Dauber et al., 2005), all point to the unsustainability of current RIL practices, and the need for reassessment of anthropogenic disturbance processes employed in these forests.

My second objective for this thesis was:

- To assess how anthropogenic disturbances in the La Chonta concession are diverging from natural disturbance, and the potential silvicultural and ecological repercussions of this divergence.

Specifically, I assessed whether there were quantifiable differences between anthropogenic and natural tree-fall gaps, and hypothesized whether the processes that are leading to these differences may have negative repercussions for the forest's ecology and concession managers. To satisfy this second objective, assessment was made of differences in the size, vegetation structure, and phenology of anthropogenic gaps and natural tree fall gaps in reduced-impact logged and unlogged forests. The further that anthropogenic disturbances diverge from their natural counterparts, the more likely that stand recovery following selective logging will take a trajectory different from that supportive of the original complement of forest biodiversity. Forest managers are therefore directly responsible for the creation of conditions that will either favour or hinder the regeneration of both ecologically and silviculturally important tree species (Lindenmayer & Franklin 2002).

1.2.3. Objective three

Anthropogenic disturbances are not necessarily limited to the direct damage caused to forest structure within logging gaps, logging roads, and skid trails. Disruption to canopy continuity associated with RIL can modify the surrounding forest's microclimate, including altering temperature, humidity, wind and light levels (Sekercioglu 2002; Houter & Pons 2005). As forest microclimatic conditions are significant determinants of forest structure (Pinard & Putz 1996b) and phenology (Justiniano & Fredericksen 2000a), there are theoretical grounds for concern that quantifiable changes to forest structure and phenology are occurring in areas of the residual stand not directly damaged by logging operations.

The third objective of this thesis was:

- To assess whether understorey vegetation found in the residual stand differs from that found in the understorey of the unharvested areas of the concession.

To satisfy the third objective, vegetation structure, floristics and phenology was studied within different habitat categories of unlogged forest and in the residual stand of harvested forest subjected to reduced-impact logging (RIL) between one and four years previously. Any differences in understorey vegetation between these two areas may indicate that logging associated changes to micro-climatic conditions are having indirect effects on regeneration beneath undisturbed areas of the residual stand. As the majority of the residual stand is left undamaged by logging, even subtle changes in the relative dominance of regenerating vegetation over these extensive areas could significantly alter what are considered to be sustainable harvest intensities.

1.3. Thesis structure

Chapters 2 and 3 are based on field work conducted during the Bolivian dry season of 2004. They examine vegetation structure, floristics and phenology in the residual stand and canopy gaps of the harvested and unharvested areas of the concession. The results from bird surveys conducted in the forestry concession in 2003/2004 are presented in Chapter 4. Chapter 5 quantifies differences in bird community composition and abundance between the harvested and unharvested areas of the concession. Chapter 6 unites the results of Chapters 2, 3, and 5 to determine whether bird communities respond to differences in particular vegetation categories created by logging disturbance. Chapter 7 concludes the main part of the thesis and provides a brief synthesis of earlier chapters.

Following the main part of the thesis, one further manuscript is attached in Appendix 1. This manuscript is indirectly related to the core theme of the thesis, and was written during the course of the PhD. Hence it is included for completeness. Appendix 1 presents observations and sonograms made of previously unrecorded displays of the Reddish hermit (*Phaethornis ruber*) hummingbird. Finally, Appendix 2 includes a map of the general location where field work was conducted and of the overall study design. This appendix also contains photographs of the research camp we built within the La Chonta concession. Prior to each Chapter are photographs depicting representative examples of birds species, different vegetation types and natural and anthropogenic disturbances found within the La Chonta concession. The reader may like to refer to these when reading the thesis. Because the primary chapters of this thesis are manuscripts developed for independent publication in scientific journals, some repetition between chapters was unavoidable.

Photo by Kristen Evans

Logging gap with sawn butttress roots of a *Ficus boliviana*. *Heliconia* sp. and other pioneer vegetation taking advantage of the new conditions.

Chapter 2

VEGETATION STRUCTURE, PHENOLOGY, AND REGENERATION IN THE NATURAL AND ANTHROPOGENIC TREE-FALL GAPS OF A REDUCED-IMPACT LOGGED SUBTROPICAL BOLIVIAN FOREST

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2.1. Abstract

Reduced-impact logging is a type of selective logging that incorporates a variety of techniques aimed at lowering levels of damage to the residual stand. In a Bolivian subtropical humid forest we studied differences in gap size, vegetation structure, regeneration and phenology between anthropogenic and natural gaps in a reduced-impact logged and unlogged forest. Harvesting took place between one and four years previously. Logging gaps were significantly larger than natural gaps (df 1, vr. 6.38, p=0.014) and had significantly lower coverage of lianas (df 1, vr. 8.64, p<0.01). Seedlings were more prevalent in logging gaps than in natural tree fall gaps (df 1, vr. 13.97, p<0.001), as were members of the herbaceous genus *Heliconia* (df 4, vr. 3.05, p=0.023). In larger gaps microclimatic conditions favour the regeneration of non-commercial pioneer species. We propose that ground disturbance during bole removal causes higher rates of mortality to shade-tolerant species in advanced stages of regeneration. This removes the competitive height advantage needed by shade-tolerant species to compete within gaps, and thus further promotes the opportunity for pioneer species to dominate gap regeneration. These observed differences between anthropogenic and natural tree-fall gaps are of direct importance to forest managers attempting to understand how disturbance associated with

reduced-impact logging influences the regeneration of commercial tree species in Bolivian forestry concessions. We discuss the ecological and silvicultural implications of these results.

2.2. Introduction

Disturbance is fundamental to the development, structure and composition of forest ecosystems (Attiwill 1994), and can be defined as a "rapid release or reallocation of community resources" (Sheil & Burslem 2003). Disturbance varies spatially and temporally in forests from frequent low intensity gap-forming disturbances operating at the scale of individual trees, to infrequent landscape scale high intensity events (eg. fires, severe storms) that can significantly alter entire stands (Coates & Burton 1997). Tree falls, and the gaps they create, represent a source of numerous relatively small scale autogenic disturbances within a forest that are simultaneously a source of mortality for some individual plant species and an opportunity for establishment for others (Denslow 1980a).

The species which eventually establish within a particular gap are determined both by niche partitioning and stochastic processes (Brokaw & Busing 2000; Schnitzer & Carson 2000). A fundamental axis of niche partitioning among tropical tree species is their regeneration strategy (Grubb 1977; Pacala et al., 1996), and although the regeneration strategies of different tropical trees are best represented by a continuum (Wright et al., 2003), it remains useful to distinguish the two broad niche categories of "shade tolerant" (primary) or "shade intolerant" (pioneer) species (Hartshorn 1980). Shade tolerant species are capable of germinating in the closed forest understorey where root competition is often intense, and can exist in a suppressed juvenile state for some time until improved light conditions permit further growth. In contrast, shade intolerant species almost exclusively germinate in gaps from seed, where light levels are high and root competition is reduced (Brokaw 1985).

Denslow (1980) proposed that, within a given forest community, there is a coupling between the relative commonness of different disturbance-related regeneration strategies, and the frequency of associated disturbance-derived regeneration sites. Empirical evidence supports this view that specific attributes of a given disturbance site influences the composition of the plant community that eventuates (Brokaw 1985). For example, the size of a gap influences the duration and intensity of light received (Lee 1978) and there is often a threshold size of gap below which pioneer species are not found (Hartshorn 1978; Foster & Brokaw 1982).

Although regeneration strategies are important determinants of gap partitioning by different plant species, stochastic processes, such as pre-gap advanced regeneration, can both limit the degree to which partitioning occurs and increase species diversity in gaps (Brokaw & Busing 2000).

The association between disturbance processes and the resulting plant community (Denslow 1980b) is of direct relevance to forest managers trying to ensure that selective logging is ecologically and silviculturally sustainable. With a significant proportion of the world’s forests used for timber production, and growing concern for the fate of forest biodiversity (Lindenmayer and Franklin, 2002), there have been calls for forest management to be as consistent as possible with natural disturbance processes (Lindenmayer & McCarthy 2002; Messier & Kneeshaw 2003). The further that anthropogenically-created disturbances diverge from their natural counterparts, the more likely that stand recovery following selective logging will take a trajectory different from that supportive of the original complement of forest biodiversity. Forest managers are therefore directly responsible for the creation of conditions that will either favour or hinder the regeneration needs of both ecologically and silviculturally important tree species (Lindenmayer and Franklin, 2002).

Nearly 50% of lowland Bolivia is covered by sub-tropical and tropical forests (Pacheco 1998), with almost half of these areas granted to timber concessions (Mostacedo & Fredericksen 1999). In 1996, a new forestry law was enacted to promote the sustainable harvesting of timber (Mostacedo and Fredericksen, 1999). To achieve best-management practices, reduced-impact logging techniques have gained widespread application in Bolivia and, as of 2005, concessions covering over 2.2 million hectares had obtained certification by the Forest Stewardship Council.

Reduced-impact logging incorporates a variety of techniques aimed at lowering levels of damage to the residual stand. These include directional felling, pre-harvest vine cutting, and preliminary inventories to reduce the number and density of logging roads (Heinrich 1995). Recent studies suggest that reduced-impact logging of tropical forests causes less damage to forest structure than conventional selective logging techniques (Asner et al., 2004a; Huth et al., 2004). Although RIL techniques potentially bring disturbance levels closer to natural disturbance regimes, there remains concern both from ecologists and forest managers regarding how RIL-induced changes to forest structure are likely to affect the ecological and silvicultural sustainability of harvested forests over future decades (Lugo 1999; Bojanic & Bulte 2002; Dauber et al., 2005).

We suggest that in keeping with goals to improve both timber and non-timber management of tropical forests in Bolivia, there is a need to assess: 1) short-term differences in the vegetation structure and phenology of anthropogenic gaps and natural tree fall gaps in reduced-impact logged and unlogged forests, and 2) how these differences can affect ecological and silvicultural sustainability. In this paper, we use a reduced-impact logged lowland tropical forest in Santa Cruz province, Bolivia, as a case study to examine differences between logging gaps and natural tree-fall gaps in (i) vegetation structure and phenology; (ii) density and composition of understorey regeneration; and (iii) to assess the potential silvicultural and ecological repercussions of differences between anthropogenic and natural disturbance processes.

2.3. Methods

2.3.1. Site description

Our study area was located in the lowland subtropical humid forest (Holdridge Life Zone System) of the Guarayos Forest Reserve, Departmento Santa Cruz, Bolivia. Research was conducted in the 100,000 hectare forestry concession “La Chonta”. This is owned and managed by Agroindustria Forestal La Chonta (509000 to 545000 easting, 8275500 to 824900 northing, Figure 1.). The forest varies in altitude from 230 m to 390 m with an average elevation of 320 m. The area is a continuation of the Brazilian Shield with low fertility soils consisting of oxisols, ultisols, and inceptisols (Park et al., 2005). The mean annual temperature is 25° C with a mean annual precipitation of approximately 1560 mm. The region experiences a distinct dry season from May to October during which time cold fronts can reduce temperatures to 5°C. The forest was bordered by palm savanna to the east with the southern boundary delimited by the Rio Blanco. Forest formerly occurred to the north and west of the concession, but has been extensively cleared for agriculture. Historically, the entire concession was subjected to both legal and illegal selective logging of Mahogany (*Swietenia macrophylla* King), Spanish Cedar (*Cedrela* *odorata* L.) and a few other highly valuable species 10 – 25 years prior to this study. The concession was certified by SmartWood in 1998, an independent third-party certifier endorsed by the Forest Stewardship Council.

2.5.2. Harvesting procedure

Between 60 to 70% of the concession is considered to have sufficient densities of timber to be commercially harvestable (Gil 1997). Approximately 2 500 ha is harvested annually over three contiguous 850 ha blocks (~4km x 2km), yielding 50,000 cubic meters of timber product. Eighteen commercial tree species were harvested during the time of this study (2003-2004) including *Ficus boliviana* Berg, *Hura crepitans* L., *Terminalia oblonga* Ruiz & Pavón, *Pseudolmedia laevis* Ruiz & Pavón, *Cariniana ianeirensis* Knuth, and *C. estre*llensis Raddi. Average harvest intensity was approximately 4 trees/ha (Jackson et al., 2002).

The forestry company La Chonta conducts an inventory of harvestable trees one year prior to logging. The minimum size for harvest is 50 cm diameter at breast-height (dbh) for all species except *F. boliviensis* and *H. crepitans*, which are harvested only when above 70 cm dbh. Approximately 20% of target species above minimum size for cutting are left as seed trees and future crop trees. During pre-harvesting inventory, trees selected for felling are cleared of all vines on or near the bole.

La Chonta uses a ‘fishbone’ harvesting strategy with a single primary north-south road bisecting each 850 ha block. Secondary roads and skid trails are then established and the location of these are guided by contour maps and the density of target trees as a guide. Secondary roads are generally 100-150 m apart and run in an east-west direction on either side of the primary road. Chainsaw teams trained in directional felling techniques try to reduce damage to the residual stand during logging. Removal and loading of boles is conducted using rubber-tired skidders to reduce soil compaction. It is intended that blocks be re-cut in 25 to 30 years.

2.5.3. Experimental design

We conducted vegetation structure and phenology surveys during June and July 2004 within 36 logging gaps and 36 natural tree-fall gaps in the unlogged forests of the La Chonta concession (Figure 2). In the unlogged forest, gaps were restricted to treefalls greater than 50 cm dbh as this is the minimum cut diameter in the logged forest. Phenology surveys were conducted from February to March 2004. To reduce the effects of seasonal variation, logged and unlogged areas were surveyed on alternate days, as were blocks logged in different years. Sampling points were located at least 300 m apart.

2.5.4. Measurement of vegetation structure and floristics

At each gap, the size of the canopy opening (defined as a vertical hole in the forest extending through the canopy to within two metres of the forest floor ((Schemske & Brokaw 1981), was measured using the dimensions of the major axis and minor axis. Gap area was calculated using the formula for an ellipse. Within each gap, a 20 m x 20 m quadrat was marked. Within this, all trees, palms, poles and stags were counted if part of their bole encroached on the quadrat. Poles were defined as trees less than 10 cm dbh but taller than 3 m. Stags were defined as dead trees greater than 10 cm dbh. Palms up to 3 m in height were counted. The numbers of fruiting and flowering plants were counted as part of the phenological assessment.

Three measurements of vegetation structure were taken from four equidistant markers located 7 m from the quadrat centre. To assess understorey density of vegetation, we used a 2 m rope held vertically, marked at 10 cm intervals. The rope was held in the center of the quadrat with the number of bands visible from each of the four markers counted, thereby providing an index of understorey density. Canopy height was measured at each marker using a clinometer and a laser rangefinder. Canopy cover was quantified at each marker using a densiometer.

At each of the four markers, a 2 m x 2 m plot was defined. In each plot, we estimated the percentage cover of grasses, ferns, palms, seedlings, dead wood, dirt, rock, sand, *Erythrochiton fallax* Kallunki (Rutaceae), *Heliconia* spp. (Heliconiaceae), other herbs, and vines. Vine coverage was divided into two classes: 0-1m (“vine low”) and 1-2 m above ground (“vine high”).

2.5.4. Data analysis

We used Principal Components Analysis (PCA, Jolliffe 2002) to reduce the data set to a smaller number of orthogonal axes that explained the variation in habitat structure in each of the gaps. Due to the low percentage of overall variation accounted for with the PCA, we used the conservative approach of interpreting only those eigenvalues belonging to the ‘cliff’ region of the scree plot (Cattell 1966); (Jackson 1993). General linear regression (Timm & Mieczkowski 1997) was used to determine whether treatment (logging gaps vs. natural tree-fall gaps), or time since treatment, were related to axes, with predictions from the regression model indicative of convergence with or divergence from habitat categories in the unlogged forest.

2.6. Results

Twenty-two physiognomy and phenological variables were analysed using Principal Components Analysis (Table 1). The PCA extracted three components of variation from 22 variables which accounted for 41% of the variability in the data set. Principal component I accounted for 17% of the variance and contrasted larger more open gaps with smaller gaps that contained a higher density and diversity of tree species. The vegetation parameters contrasted in PCI also distinguished logging gaps from natural tree-fall gaps. PC II accounted for a further 13% of the variability of the data set and contrasted gaps with a high percentage cover of vines, with gaps with a high percentage cover of seedlings. PC III accounted for a further 11% of the data set variability and contrasted gaps with a high cover of *Heliconia* spp. with those possessing bare ground.

Table 2 shows the means and standard errors for vegetation structure and phenology variables in natural gaps and gaps created by reduced-impact logging. Results from general linear regression demonstrated that logging gaps were significantly larger than natural gaps (df 1, variance ratio 6.38, p=0.014; Figure 3.) and were significantly lower in understorey density (df 1, vr. 4.75, p=0.033). The difference in understorey density was in part driven by reduced coverage of vines in logging gaps (df 1, vr. 8.64, p<0.01). Seedlings were more prevalent in logging gaps than in natural tree fall gaps (df 1, vr. 13.97, p<.001). Assessment using years since logging as a treatment variable demonstrated that the percentage cover for species of *Heliconia* was significantly higher in logging gaps than in natural gaps two years following logging (df 4, vr. 3.05, p=0.023) while flowering activity was significantly higher in logging gaps three years after logging (df 4, vr. 3.71, p<0.01). Canopy cover was significantly reduced in logging gaps for the first two years following logging (df 4, vr. 4.34, p<0.01), and leaf litter depth was significantly reduced in logging gaps for the first year following logging (df 4, vr. 3.07, p=0.02).

Table 2.1. Results of a Principal Components Analysis (PCA) of vegetation structure variables for logging and natural gaps (n=72) in the subtropical humid forests of the La Chonta forestry concession, Santa Cruz, Bolvivia. Results listed in descending order for principal component I (PC I).

	Logging gaps and natural tree-fall gaps		
PCA component	I	II	III
Eigenvalue	3.80	2.94	2.33
Cumulative % variance explained	17.28	30.65	41.25
Variable loadings			
# of tree species / 0.04ha	0.40	-0.12	-0.10
Canopy openness	0.37	0.20	-0.10
# of trees / 0.04ha	0.35	-0.14	0.01
Canopy height (m)	0.33	0.22	0.00
Canopy cover (%)	0.33	0.07	-0.03
# of poles / 0.04 ha	0.28	0.07	-0.24
Leaf litter depth	0.23	-0.26	0.24
Fern % cover	0.18	-0.04	0.34
Basal area sq. m. / 0.04ha	0.17	0.15	-0.03
Leaf litter % cover	0.10	-0.25	0.22
Erythrochiton fallax % cover	0.10	0.10	-0.11
Palm % cover	0.07	0.03	0.17
# Flower plants / 0.04ha	0.04	0.07	0.40
# fruiting plant / 0.04ha	0.03	-0.28	0.02
Seedling % cover	-0.01	0.28	-0.16
Understorey density (0-20)	-0.02	0.17	-0.08
# of palms / 0.04ha	-0.03	0.00	0.26
Vine high % cover	-0.04	-0.46	-0.18
Bare ground % cover	-0.10	0.17	-0.30
Vine low % cover	-0.11	-0.46	-0.23
Heliconia spp. % cover	-0.12	0.16	0.48
Gap size (m^2)	-0.31	0.18	-0.01

Table 2.2. Mean scores for 22 variables relating to vegetation structure within natural and anthropogenic gaps in the reduced impact logged area of the subtropical humid forests of the La Chonta forestry concession, Santa Cruz, Bolvivia. S.E. stands for standard error.

	Unlogged		*Logged*	
	Mean	SE	Mean	SE
# of tree species / 0.04ha	8.4	0.5	7.7	0.5
# of trees / 0.04ha	14	1	11.5	0.7
Canopy height (m)	9.8	0.8	11	0.8
Canopy cover (%)	91	1.1	88	1.5
# of poles / 0.04 ha	24.1	1.5	24.5	1.9
Leaf litter depth	2.1	0.1	1.9	0.1
Fern % cover	28.3	2.7	23.9	2.3
Basal area sq. m. / 0.04ha	0.5	0.1	0.5	0.1
Leaf litter % cover	80	1.6	79	1.8
Erythrochiton fallax % cover	5	2.3	1	0.7
Palm % cover	1.4	0.5	2.2	0.6
# Flower plants / 0.04ha	15.2	3	11.5	3
# fruiting plant / 0.04ha	1	0.3	0.4	0.1
Seedling % cover	13.3	1.7	23.6	2.2
Understorey density (0-20)	5.3	0.5	6.8	0.5
# of palms / 0.04ha	0.7	0.5	1.1	0.8
Vine high % cover	10.7	2.1	3.8	1
Bare ground % cover	4.3	0.8	3.3	0.8
Vine low % cover	19.9	2.7	13.7	1.9
Heliconia spp. % cover	15	2.5	20	3.2
Gap size (m^2)	404.5	52.4	638.2	76.9

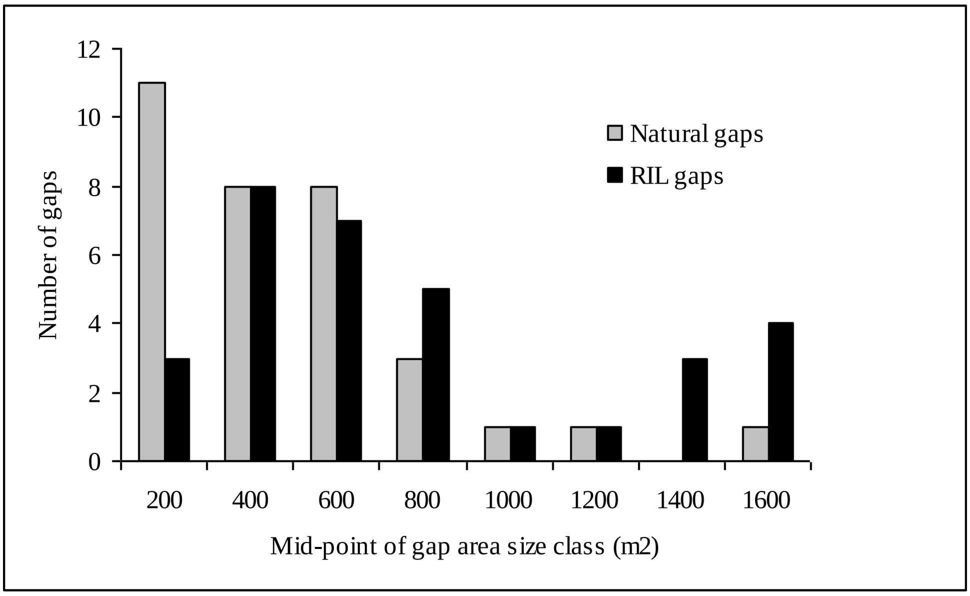

Figure 2.1. Distribution of gap sizes within the subtropical humid forests of the La Chonta forestry concession, Santa Cruz, Bolvivia.

2.7. Discussion

Anthropogenic gaps in the reduced-impact logged area of La Chonta were significantly larger than their naturally formed counterparts in the unlogged forests of the concession. The difference in size results from selective logging being an exogenous cause of mortality that targets the larger, healthy, and well-formed individuals of a forest's tree species (Auld & Bull 2003), with mortality often resulting in the bole cutting a swathe through the surrounding canopy (Whitmore 1978). Under natural conditions, the death of even the largest trees may have a relatively small impact on the surrounding canopy if mortality results in the slow deterioration of the standing tree (Howe 1990). Inevitably these differences result in selective extraction increasing the frequency of large gaps permeating a forest canopy. In addition, the size of anthropogenic gaps in the La Chonta concession was further exacerbated by the targeting of the large free-standing fig *Ficus boliviana*. This species regularly achieves a dbh of >200 cm and possesses a disproportionately large crown often exceeding 30m in diameter (A & A.M. Felton pers obs). In our study, felling of *F. boliviana* was responsible for the majority of gaps over 1000 m^2, including four that exceeded 1500 m^2.

Of concern to forest managers is the association between forest disturbance and liana infestation. Lianas depend on the physical support of other plants and their presence is known to inhibit tree regeneration, restrict the growth rates of tree seedlings, and reduce the economic value of commercial trees through an associated increase in stem deformation (Carse et al., 2000). Lianas generally increase in density after natural and anthropogenic forest disturbance (Hegarty & Caballé 1991), and thrive in unmanaged timber operations (Pinard & Putz 1994). Lianas are of special concern to managers of Bolivian tropical forests where some of the highest liana densities in the world have been found (Pérez-Salicrup et al., 2001). To reduce the economic cost of lianas, and to minimize "domino" tree-falls while harvesting, managers at La Chonta employ pre-harvest liana cutting which involves the cutting of lianas within a 30 m radius of the bole of target trees approximately one year prior to logging (Alvira et al., 2004). As we found significantly fewer lianas in logging gaps than in natural tree fall gaps, it appears that the technique of pre-harvest liana cutting is effective at reducing liana proliferation, at least over the four years subsequent to harvest. Our results concur with Gerwing and Uhl's (Gerwing & Uhl 2002) study from the Brazilian Amazon, which also found that pre-logging liana cutting significantly reduced liana densities in logging gaps. Part of the reason for reducing liana density is to induce a concomitant increase in seedling density. As seedling densities were higher in logging gaps, our results suggest that liana reduction is helping to promote tree seedling regeneration. However, as the density of tree seedlings also can increase with both disturbance (Fredericksen & Mostacedo 2000), and gap size (Orians 1983), increased seedling densities in logging gaps may be the outcome of several factors. Although the increase in seedling regeneration is a positive result for forest managers, findings suggest that few of them are likely to belong to commercial species.

The larger a gap in the canopy, the further local microclimatic conditions can be altered, including (but not limited to) changes to the availability of photosynthetically active radiation, heat fluxes, wind and humidity levels (Pinard & Cropper 2000; Asner et al., 2004b). These microclimatic conditions are resource axes that can be competitively partitioned among colonizing plant species, with some species being favoured or disadvantaged at different points along the gap-size gradient (Denslow 1980a). In our study, members of the genus *Heliconia* had significantly higher densities in logging gaps, and thus appear to benefit from microclimatic conditions associated with decreased canopy cover and increased gap size. *Heliconia* is a large, primarily Neotropical genus (200-250 spp.) of rhizomatous, herbaceous perennials. They are common occupants of areas characterized by high solar radiation (Rundel et al., 1998).

Higher levels of radiation are commonly associated with increased reproductive activity in understorey plants (Costa & Magnusson 2003). We found that this pattern was most noticeably reiterated by the abundant flower production of *Heliconia* spp. in logging gaps three years after harvest. We observed two species of hummingbird (Reddish hermit *Phaethornis ruber* L. and White-chinned sapphire *Hylocharis cyanus* Vieillot) regularly visiting the flowers of both *Heliconia* spp and *Costa* spp in natural and anthropogenic gaps (A. Felton pers. obs.). The increased provision of nectar by these and other understorey plant species in logging gaps may go some way to offsetting the loss of alternative sources of food (eg. epiphytes on felled trees) for nectarivores (Grieser Johns 1997). Unfortunately, it is also possible that the rapid colonization of logging gaps by understorey herbaceous species such as *Heliconia* spp. may limit commercial tree species regeneration (Attiwill 1994; Fredericksen & Mostacedo 2000).

Insufficient regeneration of commercial tree species in Bolivian forestry concessions is of significant concern to forest managers and ecologists (Mostacedo & Fredericksen 1999; Jackson et al., 2002). In the logging gaps of La Chonta, regeneration is dominated by non-commercial pioneer species, at the expense of shade tolerant commercially valuable species such as *Batocarpus amazonicus* Ducke, *Pseudolmedia laevis,* and *Ampelocera ruizii* Klotzsch (Park et al., 2005). Because pioneer species regenerate predominantly in larger gaps (Brokaw 1985), some researchers have suggested the adoption of logging techniques that create smaller disturbances, thereby promoting the regeneration of shade-tolerant species (Park et al., 2005), and reducing the likelihood of pioneer invasion (Brokaw 1985; Uhl et al., 1988). We suggest that although the size of logging gaps is an issue that needs to be addressed, problems with the regeneration of shade-tolerant species also may result from more fundamental differences between logging gaps and natural tree-fall gaps.

Studies in natural tree-fall gaps of unmanaged forests suggest that although the regeneration requirements of some tree species are adapted to different gap microenvironments, resultant gap partitioning by species under natural conditions is often overridden or blurred by stochastic events that can both limit partitioning and promote diversity in gaps (Brokaw & Busing 2000). These authors contend that a principle stochastic driver of this diversity is pre-gap advanced regeneration. Juveniles of shade tolerant species that are present prior to the formation of the gap, and survive gap formation, can dominate gap regrowth simply by being the tallest individuals at the time of disturbance (Brown & Jennings 1998; Hubbell et al., 1999). In this way stochasticity acts as a “keystone process”, promoting higher diversity in gaps by reducing the competitive advantage of a few individual pioneer species better adapted to microclimatic conditions in that particular gap.

In Bolivian forestry concessions, the reasons for recruitment failure of commercial tree species include insufficient seed trees, poor seed viability, high seed predation, and excessive interplant competition (Mostacedo & Fredericksen 1999; Pariona et al., 2003). We suggest that in addition to these problems, logging gaps lack adequate regeneration of shade-tolerant commercial species because extensive disturbance of soils by skidders during bole removal (Jackson et al., 2005) causes the mortality of shade-tolerant species in advanced stages of regeneration achieved prior to gap formation. This removes the competitive height advantage needed by shade-tolerant species to compete within gaps, and emphasizes the advantage of pioneer species possessing faster growth rates within the favourable microclimatic conditions of large gaps (Brokaw, 1985). It is our view that this process is at least partly causes domination of logging gaps by regenerating pioneer species.

There are a number of repercussions for silviculture if this conclusion is proved to be correct. First, estimates of how small logging gaps have to be to avoid dominance by shade-intolerant species may be inaccurate if they are based solely on literature from studies of natural regeneration in tree-falls from unmanaged tropical forests. Second, the benefits of soil scarification, as a means of promoting the regeneration of certain species (eg. *Schizolobium amazonicum*), need to be weighed against the increased risk of invasion by non-commercial pioneers. Studies of scarified logging gaps have found that subsequent regeneration was dominated by early successional tree species (Fredericksen & Pariona 2002). Third, if stochasticity is acting as a keystone process that serves to promote tree species diversity, then weakening this process will be of concern to those trying to ensure silvicultural techniques maintain commercial tree species abundance in Bolivian forestry concessions.

2.7.1 Management implications

Our research suggests that pre-harvest liana cutting is successful at reducing liana density for at least several years after logging. This procedure also appears to be an effective means of increasing the percentage cover of tree seedlings in logging gaps. However, current silvicultural practices (specifically the harvesting of *Ficus boliviana*) are potentially negating the benefits of increased seedling density by creating large gaps with microclimatic conditions preferentially beneficial to the regeneration of non-commercial pioneer species. We propose that this problem can be further exacerbated through damage to shade-tolerant species in advanced stages of regeneration during tree felling and bole removal. We suggest that research is needed to quantify the damage caused to commercial tree species in advanced stages of regeneration from each component of the felling and bole removal process. If subsequent research confirms that these processes are aiding regeneration dominance by pioneer species, then forest managers may need to increase supervision and economic incentives for tree fellers and skidder operators to recognize and reduce damage to commercial tree species in advanced stages of regeneration. The more technically challenging solution of species-specific site preparation, and enrichment planting, may also be needed (Mostacedo & Fredericksen 1999).

Regardless of the precise nature of the solution, the dominance of non-commercial pioneers in logging gaps (Park et al., 2005), lack of adequate regeneration for most commercial species (Pariona et al., 2003), and current projections of dramatic declines in the volume of future harvests (Dauber et al., 2005), all point to the unsustainability of current reduced-impact logging practices, and the need for reassessment of anthropogenic disturbance processes employed in these forests.

2.8. Acknowledgements

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Forest giant *Ficus boliviana* Photo by Kristen Evans

Chapter 3

SHORT TERM UNDERSTOREY PLANT RESPONSES TO INDIRECT DISTURBANCE IN THE RESIDUAL STAND OF A REDUCED-IMPACT LOGGED BOLIVIAN SUBTROPICAL FOREST

3.1. Abstract

In a Bolivian subtropical humid forest vegetation structure, floristics and phenology was studied within different habitat categories of unlogged forest and in the residual stand of harvested forest subjected to reduced-impact logging (RIL) between one and four years previously. The unlogged forest and the residual stand of the harvested forest were similar in terms of floristic composition. However, there was a significant difference in understorey vegetation structure and phenology between the unlogged forest and the residual stand four years after harvesting (t=-2.34, P<0.05). Four years after logging the residual stand of the RIL forest had a significantly higher percentage cover of seedlings (t=2.48, P=0.014) and palms (t=2.33, P=0.021) than their unlogged counterparts. In contrast the percentage cover of ferns (t=-2.49, P=0.014) and the number of plants in flower (t=-2.13, P=0.034) was significantly lower in the understorey of the residual stand four years following harvesting. The possibility that understorey vegetation in the residual stand was proceeding along a different successional trajectory from that found within the unlogged forest is raised. Alternative hypotheses are also raised, as are the potential ecological and silvicultural implications of these results. As the majority of the residual stand was left undamaged by logging, even subtle changes in the relative dominance of regenerating vegetation over these extensive areas could significantly alter what are considered to be sustainable harvesting intensities.

3.2. Introduction

It is estimated that two-thirds of the world’s species are directly dependent upon tropical forests, despite their covering only 10% of the Earth’s land surface (Groombridge & Jenkins 2002). Thus, even localized anthropogenic disturbances to these forest ecosystems can potentially lead to significant impacts on global biodiversity. Selective logging is of concern to those assessing causal mechanisms behind the degradation of tropical forests, due to the vast areas that are now known to be degraded by this land-use (Asner et al., 2005). The largest remaining tracts of tropical forest occur in Latin America (FAO 2001), and by the mid-1990s an estimated 28% of these forests had been commercially logged (Johns & Skorupa 1987). Minimizing the damage caused by commercial logging of tropical forests worldwide, and more specifically in Latin America, is therefore a global conservation priority (Nepstad et al., 1999).

Reduced-impact logging (RIL) incorporates a variety of techniques aimed at lowering levels of damage to the residual stand. These include directional felling, pre-harvest vine cutting, and preliminary inventories to reduce the number and density of logging roads (Heinrich 1995). Reduced-impact logging of tropical forests can result in substantially less damage to the residual stand than conventional selective logging techniques (Asner et al., 2004a), and simulation studies support assertions that RIL lowers the ecological damage to forests (Huth et al., 2004). Although RIL techniques potentially bring disturbance levels closer to natural disturbance regimes, there remains concern from both ecologists and forest managers regarding how RIL-induced changes to the structure of a forest are likely to affect their ecological and silvicultural sustainability over future decades (Lugo 1999; Bojanic & Bulte 2002; Dauber et al., 2005). As a result of these and similar concerns, a substantial amount of research has focused on: 1. Increasing our understanding of the ecology of timber species (Guariguata & Pinard 1998; Justiniano & Fredericksen 2000b, a; Brienen & Zuidema 2006), 2. Finding means of improving the regeneration rates of timber trees (Pérez-Salicrup 2001; Fredericksen & Pariona 2002; Alvira et al., 2004), and 3. Decreasing damage to the residual stand (Gullison & Hardner 1993; Jackson et al., 2002).

Residual stand damage can be defined as ‘any disturbance by logging that reduces the capacity of an area to produce a desirable future crop’ (Stehman & Davis

1997). Despite the encompassing nature of this definition, studies assessing logging-induced changes to the residual stand primarily restrict themselves to quantifying damage to trees (eg. broken limbs, exposed cambium) caused directly by logging machinery or by the felling of other trees (Bettinger & Kellogg 1993). Beyond the immediate vicinity of the skid trails and logging gaps, there are a number of less direct means by which logging activities may alter the ecological and economic trajectory of a forest, primarily as a result of changes to canopy continuity.

In the humid forests of the Neotropics, natural disturbance may leave approximately 10% of the forest canopy opened by tree falls at any one time (Sanford et al., 1986; Uhl et al., 1988). Canopy disturbance in a selectively logged forest, however, can be several times greater than this background level (Uhl & Vieira 1989; Jackson et al., 2002). With increasing harvest intensity, more of the forest canopy is opened by tree fall gaps and a greater proportion of the remaining stand is close to these canopy openings (Panfil & Gullison 1998). These disruptions to canopy continuity modify the immediate forest's microclimate including altering temperature, humidity, wind and light levels (Sekercioglu 2002; Houter & Pons 2005). As forest microclimatic conditions are significant determinants of forest structure (Pinard & Putz 1996b) and phenology (Justiano & Fredericksen 2000b), there is theoretical support for examining whether quantifiable changes to forest structure and phenology are occurring in areas of the residual stand not directly damaged by the creation of skid trails and logging gaps.

Nearly 50% of lowland Bolivia is covered by sub-tropical and tropical forests (Pacheco 1998), with almost half of these areas granted timber concessions (Mostacedo & Fredericksen 1999). In 1996, a new forestry law was enacted to improve forestry policy and enforcement (Fredericksen 2000). Specifically, the law promoted the sustainable harvesting of timber using best-management practices including pre-harvest inventories, management plans and the protection of biological reserves within concessions (Mostacedo & Fredericksen 1999). To achieve best-management practices, reduced-impact logging techniques have gained widespread application in Bolivia and, as of 2005, concessions covering more than 2.2 million hectares have obtained certification by the Forest Stewardship Council (FSC).

We suggest that in keeping with goals to improve both timber and non-timber management of tropical forests in Bolivia, there is a need to assess changes to forest structure and phenology in the residual stand of reduced-impact logged forests and to assess how these changes may alter their long-term ecological and economic sustainability. In this paper we use a reduced-impact logged subtropical forest in the Department of Santa Cruz, Bolivia, as a case study to examine (i) understorey regeneration within the residual stand; (ii) phenological differences in the residual stand; and (iii) to assess the potential ecological and silvicultural repercussions of any differences from the unlogged forest. We discuss the ecological and silvicultural implications of these results and how any observed differences are of direct importance to forest managers attempting to improve the regeneration rates for commercial tree species in Bolivian forests.

3.3. Methods

3.3.1. Site description

Our study area was located in the lowland subtropical humid forest (Holdridge Life Zone System) of the Guarayos Forest Reserve, Departmento Santa Cruz, Bolivia. Research was conducted in the 100,000 hectare forestry concession “La Chonta”, owned and managed by Agroindustria Forestal La Chonta (509000 to 545000 easting, 8275500 to 824900 northing; Figure 1). The forest varies in altitude from 230 m to 390 m with an average elevation of 320 m. The area is a continuation of the Brazilian Shield with low fertility soils consisting of oxisols, ultisols, and inceptisols (Park *et al.* 2005). The mean annual temperature is 25°C with a mean annual precipitation of approximately 1560 mm. The region experiences a distinct dry season from May to October during which time cold fronts can reduce temperatures to 5°C. The forest was bordered by palm savannah to the east with the southern boundary delimited by the Rio Blanco. Forest formerly occurred to the north and west of the concession, but has been extensively cleared for agriculture. The entire concession was subjected to legal and illegal selective logging of mahogany (*Swietenia macrophylla* King), and Spanish cedar (*Cedrela odorata* L.) 10 – 25 years prior to this study. The concession received FSC-standard certification in 1998.

3.5.2. Harvesting procedure

Between 60 to 70% of the concession is considered to have sufficient densities of timber to be commercially harvestable (Gil 1997). Approximately 2,500 ha is annually harvested over three contiguous 850ha blocks (~4km x 2km), yielding 50,000m^3 of timber product. Eighteen commercial tree species were harvested during the time of this study including *Ficus boliviana* C.C. Berg, *Hura crepitans* L., *Terminalia oblonga* Ruiz & Pavón, *Pseudolmedia laevis* Ruiz & Pavón, *Cariniana ianaerensis* R. Knuth, and *C. estrelliensis* Raddi. Average harvest intensity was approximately 4 trees/ha (Jackson et al., 2002).

The forestry company La Chonta conducts an inventory of harvestable trees one year prior to logging. The minimum size for harvest is 50cm diameter at breast-height (dbh) for all species except *F. boliviana* and *H. crepitans*, which are harvested only when above 70cm dbh. One in five harvestable trees is required by law to be left as a seed tree. During pre-harvesting inventory, trees selected for felling are cleared of all vines on the bole.

La Chonta uses a ‘fishbone’ harvesting strategy with a single primary north-south road bisecting each 850ha block. Secondary roads and skid trails are then established using contour maps and the density of target trees as a guide. Secondary roads are generally 100-150m apart and run in an east-west direction on either side of the primary road. Chainsaw teams trained in directional felling techniques try to reduce damage to the residual stand during felling. Removal and loading of boles is conducted using rubber-tired skidders to reduce soil compaction. It is intended that blocks be re-cut in 25 to 30 years.

3.5.3. Experimental design

Vegetation structure and floristic surveys were conducted during June and July 2004 within 216 samplings points distributed throughout the residual stand areas of the logged forest, and unlogged areas of the concession that supported commercial densities of harvestable timber (Figure 2). Because selective logging disproportionately disturbs forest with commercial densities of harvestable trees, a random survey of the residual stand in harvested blocks was unlikely to sample habitat directly comparable to that found within the unlogged forest blocks. A stratified sampling design was therefore used which incorporated both commercial tree species occurrence, and vegetation height. This design increased the likelihood that logged and unlogged sampling points were comparable in terms of habitat type, and accounted for natural variation in vegetation structure. The three habitat categories used were: 1. “target” forest (T) with vegetation height over 20m and possessing one of five commercial tree species (*Ficus boliviana, Hura crepitans, Cariniana estrellensis, C. ianeirensis, Terminalia oblonga*) of harvestable size, 2. “future” target forest (F) from 12-20m in height and possessing a commercial tree of the afore mentioned five species not yet of harvestable size but above 30cm dbh, and 3. “non-target” forest (N) of less than 12m in height and not possessing commercial tree species above 10cm dbh.

In the unlogged forest, 9 survey points, representing three of each of the three habitat categories, were randomly chosen from available alternatives (as identified during preliminary vegetation surveys) and located along three ~1 km long transects (see Figure 2). This design was repeated until 108 survey points were designated for the unlogged area. The equivalent survey design was repeated in the logged forest for the total of 216 survey points used in the study. In the logged forest, the harvestable tree in the ‘target’ category was represented by a seed tree left by loggers to aid regeneration. Trees that were not harvested due to undesirability (eg. insufficient bole length or malformation) were not included in this category. Phenology surveys were conducted from February to March 2004, and phenological results are interpreted acknowledging the limited period of our sampling. To reduce bias caused by seasonal variation, logged and unlogged areas were surveyed on alternate days, as were blocks logged in different years. All points were located at least 15 m away from skid trails or logging gaps, and at least 250 m away from logging roads.

3.5.4. Measurement of vegetation structure and floristics

At each point, a 20m x 20m quadrat was marked within which all trees, palms, poles and snags were counted if part of their bole encroached on the quadrat. Trees (>10cm dbh) were identified to species-level by botanists from the Instituto Boliviano de Investigación Forestal (IBIF). Poles were defined as trees less than 10cm dbh but taller than 3m. Snags were defined as dead trees greater than 10cm dbh. Palms up to 3m in height were counted, with palms over this height also identified to species. The numbers of fruiting and flowering plants were counted as part of the phenological assessment.

The following measurements of vegetation structure were taken from four equidistant markers located 7m from the quadrat center. To assess understorey density of vegetation, we used a 2m rope held vertically from the ground, marked with 1cm bands of fluorescent tape at 10cm intervals. The rope was held in the center of the quadrat with the number of bands visible from each of the four markers counted, thereby providing an index of understorey density. Canopy height was measured at each marker using a clinometer to obtain a true vertical angle and a laser rangefinder to measure distance. Canopy cover was quantified at each marker using a densiometer with an average calculated from north, south, east and west readings. At each of the four markers, a 2m x 2m plot was defined. In each plot, the percentage cover of grasses, herbs, ferns, palms, vines, seedlings, *Erythrochiton fallax* Kallunki (Rutaceae), *Heliconia* spp. (Heliconiaceae), dead wood, exposed soil, rock, and sand was estimated. Vine coverage was divided into percentage cover from ground level to one meter (vine low), and percentage cover from one to two meters above ground (vine high).

3.5.5. Data analysis

Principal Components Analysis (PCA) was used to reduce the data set to a smaller number of orthogonal axes that explained the variation in habitat structure in each of the 20m x 20m quadrats for the three habitat categories. Due to the low percentage of overall variation accounted for with the PCA, we used the conservative approach of only interpreting those eigenvalues belonging to the ‘cliff’ region of the scree plot (Cattell 1966; Jackson 1993). General linear regression (Timm & Mieczkowski 1997) was used to determine whether time since treatment, were related to axes, with predictions from the regression model indicative of convergence with or divergence from habitat categories in the unlogged forest.

Correspondence analysis (Greenacre 1984) was used to determine whether there were differences in tree species composition and abundance between the logged and unlogged areas. Only tree species with at least fifteen individuals (>10cm dbh) were included in this analysis. A Sørensen’s quotient of similarity (Southwood & Henderson 2000) was conducted to determine the percentage similarity in tree diversity between the unlogged and logged areas.

3.6. Results

Scree plot assessment of PCA results suggested that interpretation was appropriate for the first two axes. The first two axes of PCA explained 19%, and

14% of the variation respectively. Loading factors from principal component one (PC I) formed a gradient from canopy openness (+), canopy height (+) and basal area (+) to vine cover (-) and leaf litter density (-) (Table. 1). Variables that loaded highly on PC II were leaf litter cover (+), understorey density (+), number of poles (+), *E. fallax* % cover (-), exposed soil % cover (-) and number of plants in flower (-). Habitat categories (target, non-target, future) were based on structural features of the forest and predictably accounted for a significant amount of the structural variation in PC I (v.r. 114.85, df 2, P<0.001). From 1 to 3 years post logging we did not detect a difference between the forest structure of the residual stand and the unlogged forest (ysl 1, t=.-.41, P>0.05; ysl 2, t = -1.78, P>0.05; ysl 3, t = 0.53, P>0.05). However, four years post logging, forest structure in the residual stand of the harvested forest significantly differed from the unlogged forest (t = -2.34, P<0.05). The residual stand of the forest logged four years previously had a significantly higher percentage cover of seedlings (t=2.48, P=0.014) and palms (t=2.33, P=0.021) than their unlogged counterparts. In contrast the percentage cover of ferns (t=-2.49, P=0.014) and the number of plants in flower (t=-2.13, P=0.034) was significantly lower in the understorey of the residual stand four years following harvesting. Variation in PC II was not accounted for by either treatment (v.r. 0.5, df 1, P=0.48) or category (v.r. 0.39, df 2, P=0.68) factors.

The study area was dominated by the tree species *Pseudolmedia laevis*, *Terminalia oblonga*, *Ampelocera ruizii*, *Urera baccifera* and members of the *Ocotea* genus. There was a 96% overlap in tree species diversity between the residual stand of the logged forest, and unlogged forest, as calculated using Sørensen’s quotient of similarity. Analysis of variance of row scores I (v.r. 0.91, df 1, P>0.05), II (v.r. 3.4, df 1, P>0.05), and III (v.r. 3.2, df 1, P>0.05) from the correlation analysis performed on tree species composition and abundance showed no significant difference in floristics between the residual stand and unlogged forest for the habitat categories considered.

Table 3.1. Results of a Principal Components Analysis (PCA) of vegetation structure variables for target (T), non-target (N) and future target (F) forest categories (n=214).

	Structural categories (T, N, F)	
PCA component	I	II
Eigenvalue	4.04	2.852
Cumulative % variance explained	19.24	32.82
Variable loadings		
Canopy openness	0.40	0.09
Canopy height (m)	0.40	0.02
Basal area sq. m. / 0.04ha	0.35	0.02
Fern % cover	0.21	0.16
# Flower plants / 0.04ha	0.17	-0.28
# fruiting plant / 0.04ha	0.15	-0.08
Understorey density	0.15	0.29
Heliconia spp. % cover	0.15	-0.13
# of palms / 0.04ha	0.13	-0.16
# of trees / 0.04ha	0.12	0.27
Canopy cover	0.12	0.28
Exposed soil % cover	0.09	-0.31
Palm % cover	0.08	-0.12
Erythrochiton fallax % cover	0.04	-0.31
# of tree species / 0.04ha	0.03	0.28
Seedling % cover	-0.02	0.18
# of poles / 0.04 ha	-0.03	0.32
Leaf litter % cover	-0.09	0.32
Leaf litter depth	-0.18	0.29
Vine high % cover	-0.38	-0.04
Vine low % cover	-0.40	-0.06

3.7. Discussion

Comparison of unharvested areas of the residual stand, with unlogged areas of the concession, revealed a relative homogeneity in tree species composition within the habitat categories considered. With regard to forest structure, concordance with the unlogged forest is only seen in areas three years or less following logging. Four years following logging several parameters representing measures of understorey vegetation in the residual stand differed significantly from those measurements made within the unlogged forest. We put forward the working hypothesis that this difference may result from a larger proportion of the forest being close to disturbance throughout the residual stand. The associated changes to microclimate may thus favor or hinder the prevalence of some plant taxa, with quantifiable differences detected given sufficient time (ie. four years in this case).

Before pursuing this line of reasoning there is one alternative possibility that first needs to be addressed. Blocks are harvested systematically in the La Chonta concession resulting in a coupling of temporal and spatial disturbance with the earlier logged blocks located to the east or south. As this pattern overlays time since disturbance with location, we cannot isolate either factor from the other. As such we accept the possibility that differences observed four years subsequent to logging could solely be the product of an *a priori* spatial variation in vegetation. However, several factors do not lend support to this hypothesis. First, observed differences in forest structure were restricted to parameters that were responsive to short term disturbances (eg. fern cover, seedling cover). No significant difference was seen in variables more indicative of fundamental spatial variability in forest structure, such as tree species diversity, or basal area. Second, tree species composition and abundance was consistent between the unharvested areas of the residual stand and the unlogged forest. Third, differences in the percentage ground cover of palms was not reiterated by counts of older palm species greater than 3m in height; possibly indicating that these differences are the result of recent processes. For these reasons, we believe it is appropriate to consider hypotheses that involve logging-induced changes to forest structure.

Four years after reduced-impact logging, the percentage cover of seedlings and small palms was higher in the logged area while there was lower fern cover and fewer plants in flower. It is possible that within the logged area, the increased proportion of forest close to disturbance is driving these changes in the understorey. Jackson et al. (2002) assessed the short-term direct impacts of logging operations on forest structure at La Chonta. They concluded that skid trails, logging roads and log landings disturbed 25% of ground area with an additional 25% of the canopy opened due to tree felling. They estimated that, in total, almost 46% of the residual stand was damaged by logging (Jackson et al., 2002). A significant proportion of the residual stand was therefore more proximate to disturbance than in the unlogged forest. This increased proximity to canopy discontinuity may result in changed micro-climatic conditions including (but not limited to) altered availability of photosythetically active radiation, heat fluxes, wind and humidity levels (Pinard & Cropper 2000; Asner et al., 2004b). These differences could be important contributors to the changes to vegetation structure observed in this study four years after logging.

Four years after logging the percentage ground cover of tree seedlings significantly increased beneath the residual stand of the logged forest, a promising result for forest managers. One of the biggest problems facing La Chonta and other Bolivian forestry concessions is insufficient timber tree regeneration (van Rheenen et al., 2004; Dauber et al., 2005). In one assessment, Mostacedo and Fredericksen, (1999) found that over 60% of timber trees in Bolivia were found to have inadequate regeneration rates. What is unknown is how many of the seedlings found in our study belong to commercially harvestable tree species. As a large proportion of the commercial trees regenerate successfully on pristine forest floor, including high value species such as *Cariniana ianeirensis* and *C. estrellensis* (Park et al., 2005), then at least some of the observed increase in seedling germination may contribute to commercial tree species regeneration. Certainly more studies are needed before any conclusions can be drawn.

Members of the Palmae appear to also benefit from germination conditions found on the forest floor of the four year old residual stand. Our result is consistent with other studies of post-logging forest recovery in gaps in Bolivia, with palms representing many of those species found to have adequate regeneration (Mostacedo & Fredericksen 1999). Although not of direct economic consequence to forestry managers at La Chonta, palms (especially arborescent species) play a vital role as providers of fruits and nuts to a wide variety of forest wildlife, including Spix's guans (*Penelope jacquacu* Berlepsch), lowland tapir (*Tapirus terrestris* L.), and spider monkeys (*Ateles chamek* Humbolt) (Bodmer 1990 A & A.M. Felton pers. obs; Peres 1994b). Their importance was based, in part, on the fact that many species of palms produce fruits at a time when the fruits of dicotyledous species are rare or non-existent, and thereby provide an alternative food supply during resource bottlenecks (Terborgh 1986a; Peres 1994a).

One possible concern for forestry managers would be if the associations between palm prevalence and high liana densities found in other studies is repeated in La

Chonta. Pérez-Salicrup et al. (2001) found that in the Oquiriquia forest, Departmento Santa Cruz, Bolivia, the only factor that significantly correlated with high liana densities was a corresponding increased prevalence of palms. The authors suggest that palms and lianas co-occur because of an overlapping preference for similar environmental conditions, possibly related to the successional stage that the forest is in (Pérez-Salicrup 2001). Lianas restrict the growth rate of tree seedlings, as well as reduce the economic value of commercial trees through an associated increase in stem deformation (Carse et al., 2000). If the pattern of co-occurrence of lianas and palms is repeated in La Chonta at a later successional stage, then this could offset any benefits from an increase in tree seedling abundance beneath the residual stand.

Species of canopy tree in La Chonta generally peak in flowering and fruiting activity at the end of the dry season, a pattern repeated throughout much of the tropics (van Schaik et al., 1993; Foster 1996; Justiniano & Fredericksen 2000a). The synchronous phenology observed in the canopy may not, however, be mirrored by plant species in the understorey. Several studies have corroborated findings that sub-canopy species are less seasonal with respect to flowering and fruiting than canopy species (Frankie et al., 1974; Opler et al., 1980; van Schaik et al., 1993; Peres 1994a; Justiniano & Fredericksen 2000b). Causal hypotheses point to the insulating nature of the canopy, which reduces the extent of seasonal variation of irradiance and humidity in the understorey, and thereby increases possibility for asynchronous reproduction in understorey species (Opler et al., 1980; van Schaik et al., 1993; Justiniano & Fredericksen 2000a). We found fewer plants in flower four years after logging during the late wet season. Proximity to disturbance may have decreased the insulating effect of the surrounding canopy, leading to an increase in the synchronicity of understorey phenology or an overall decline in flowering activity. Either scenario would reduce the chance for flowering to be observed in these areas during the times that our surveys were conducted. We emphasize that our phenological results represent a snap-shot in time and therefore require further research before any conclusions can be drawn.

A decrease in the insulating effect of the surrounding canopy also may account for the lower abundance of ferns found beneath the residual stand four years after logging. Although the understorey of some temperate forests subjected to shelterwood logging can become dominated by species of bracken fern (*Pteridium aquilinum* L.), non-flowering plants including other fern species are known from these forest studies to decline in abundance following logging (Quinby 2000). In the Experimental Forest Management Station located north of Manaus Brazil, Costa and Magnusson (Costa & Magnusson 2002) found that a species of fern (*Lomariopsis prieuriana* Fée) declined in density after logging, possibly as a result of photoinhibition. As some commercial tree species are associated with environments dominated by high fern cover (eg. *Pouteria nemorosa* Baehni; Park et al. 2005), it is possible that selection against these environments will also negatively impact on availability of these tree species.

3.7.1 Management implications

The results of this study indicate that four years after reduced-impact logging, understorey vegetation in the residual stand may be proceeding along a different successional trajectory from that found within similar habitat categories in unlogged forest. The possibility of an eventual increase in seedling density within harvested blocks is a positive sign, but a result we argue is in urgent need of further research for its true implications to be adequately understood. As 54% of the residual stand was left undamaged by logging (Jackson et al., 2002), even subtle changes in the relative dominance of regenerating vegetation over these extensive areas could significantly alter what are considered to be sustainable harvesting intensities. If an overall increase in proximity to disturbance is driving the observed differences in the understorey of the residual stand, then any resultant repercussions are likely to be enhanced in the future as more tree species become commercially valuable and a greater proportion of the canopy is opened (Panfil & Gullison 1998; Park et al., 2005).

To our knowledge, this is the first study to assess changes in the understorey vegetation of the residual-stand in a tropical forest subjected to reduced-impact logging. We see our results and accompanying working hypotheses as preliminary, and suggest that assessment of the understorey vegetation structure and phenology of the residual stand is an important area for future research within tropical RIL forestry concessions.

3.8. Acknowledgements

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Photo by Helga Peters

White-fronted Nunbird (*Monasa morphoeus*)

Chapter 4

BIRDS SURVEYED IN THE HARVESTED AND UNHARVESTED AREAS OF A REDUCED-IMPACT LOGGED FORESTRY CONCESSION, LOCATED IN THE LOWLAND SUBTROPICAL HUMID FORESTS OF THE DEPARTMENT OF SANTA CRUZ, BOLIVIA.

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4.1. Abstract

As part of a larger study of reduced-impact logging effects on bird community composition, we surveyed birds from December to February during the 2003-2004 wet-season within harvested and unharvested blocks of the La Chonta forestry concession, Department of Santa Cruz, Bolivia. The logged forest was harvested using reduced-impact logging techniques between one and four years previously. During point count surveys, we identified 5 062 individual birds, belonging to 155 species, and 33 families. We provide a list of bird species found within the harvested and unharvested blocks of the concession for the benefit of other researchers assessing the responses of Neotropical avifauna to disturbance, and to facilitate increased understanding of the diverse bird assemblages found within the lowland subtropical humid forests of Bolivia.

4.2. Introduction

There are over 1 400 species of birds known from Bolivia, with the majority of species found in the sub-tropical and tropical forests of lowland Bolivia (Pacheco 1998). Almost half of forests in lowland Bolivia are now granted to forestry concessions (Mostacedo & Fredericksen 1999). In 1996, a new forestry law was enacted to promote the sustainable harvesting of timber (Mostacedo & Fredericksen 1999). To achieve best-management practices, reduced-impact logging techniques have gained widespread application in Bolivia and, as of 2005, concessions covering over 2.2 million hectares had obtained certification by the Forest Stewardship Council (FSC 2005). Here, we provide the results of a wet season bird survey of the harvested and unharvested areas on one of these certified concessions located in the lowland subtropical humid forests of the Department of Santa Cruz, Bolivia.

4.3. Methods

4.3.1. Study site

Our study area was located in the lowland subtropical humid forest of the Guarayos Forest Reserve, Department of Santa Cruz, Bolivia. Research was conducted in the 100 000 ha forestry concession “La Chonta”. This is owned and managed by Agroindustria Forestal La Chonta (509000 to 545000 easting, 8275500 to 824900 northing; Figure 1.). The forest has an average elevation of 320 m (range 230-390m). The soils consist of oxisols, ultisols, and inceptisols (Park et al., 2005). The mean annual temperature is 25° C with a mean annual precipitation of approximately 1 560 mm. The region experiences a distinct dry season from May to October. The entire concession was subjected to legal and illegal selective logging of mahogany (*Swietenia macrophylla*), and Spanish cedar (*Cedrela odorata*) from ~1980 to 1995. The concession was certified by SmartWood in 1998.

4.3.2. Harvesting procedure

Approximately 2 500 ha of forest is harvested annually over three contiguous 850 ha blocks (~4 km x 2 km), yielding 50 000 m^3 of timber. Eighteen tree species were harvested during the time of this study (2003-2004) including *Ficus boliviana*, *Hura crepitans*, *Terminalia oblonga*, *Pseudolmedia laevis*, *Cariana ianeirensis*, and *C. estrellensis*. Average harvest intensity was approximately 4 trees per ha (Jackson et al., 2002). The forestry company Agroindustria Forestal La Chonta conducts inventories of harvestable trees one year prior to logging. The minimum size for harvest is 50 cm diameter at breast-height (dbh) for all species except *F. boliviensis* and *H. crepitans,* which are harvested above 70 cm dbh. One in five harvestable trees is required by law to be left as a seed tree. During pre-harvesting inventory, trees selected for felling are cleared of all vines from their bole.

The forestry company uses a ‘fishbone’ harvesting strategy with a single primary north-south road bisecting each 850 ha block. Skid trails are located 100-150 m apart and run in an east-west direction on either side of the primary road. Chainsaw teams trained in directional felling techniques try to reduce damage to the residual stand during logging. Removal and loading of boles is conducted using rubber-tired skidders to reduce soil compaction. It is intended that blocks be re-cut in 25 to 30 years.

4.3.3. Survey design

A stratified-random sampling design was used. The strata to guide site selection included commercial tree species occurrence, vegetation height, and disturbance type. Five habitat types were surveyed including: 1. ‘Tall forest’ points (T) with vegetation height over 20 m and possessing one of five commercial tree species (*Ficus boliviensis*, *Hura crepitans*, *Cariniana estrellensis*, *C. ianeirensis*, *Terminalia oblonga*) of harvestable size; 2. ‘Medium forest’ points (F) from 12-20 m in height and possessing a commercial tree of the afore mentioned five species not yet of harvestable size but above 30 cm dbh; 3. ‘Vine thicket’ points (N) of less than 12m in height and not possessing commercial trees above 10 cm dbh; 4. ‘Gap’ points (G) possessing a tree-fall gap caused by the felling of a tree (in the harvested blocks) or a natural tree fall (in the unlogged blocks) of greater than 50 cm dbh; and 5. ‘Road’ points (R) located on a primary north-south logging road in the logged forest, or along the main north-south access path in the unlogged forest. In total, 360 points was surveyed, equally distributed between the logged and unlogged forest, represented by 72 points of each of the five habitat categories.

4.3.4. Bird surveys

At each of the 360 survey points, we used an unlimited distance point-count method of surveying bird species abundance. All survey points were located at least 300 m from the nearest point, and at least 500 m from the edge of neighbouring treatment blocks. Surveys were conducted from December to February of the 2003-2004 wet season. Surveys began at first light (5:45-6:00 am), and continued until approximately 10:45 am. Counts were not undertaken if weather was poor (eg. rain, high wind). This period overlapped with the daily peak in bird vocal activity. A day's survey consisted of visiting three points of each of the five habitat types (15 points in total). Each point was surveyed for 12 minutes. We included birds flushed from the survey point on approach by the observer, while birds flying over the survey area were not included in the analysis.

Due to the density of forest vegetation, most identifications were made acoustically, rather than visually. In addition to point counts, recordings of birds were made using a Sony TCM 5000 tape-recorder that was attached to a Sennheiser ME66 microphone. These recordings were used as a supplement to in-the-field identification of vocalizing species. For unidentified species, symbolic representations of songs were noted. This was in addition to notes on the recording time, direction, and estimated distance to the call. This enabled the matching of subsequent identifications with abundance and distance information. Unknown recordings were identified using the CD-ROM Birds of Bolivia, 2.0 (Mayer 2000), or by an expert (B.H). All research was approved by the relevant authorities and this study was conducted within the ethical guidelines of Australia and Bolivia.

4.4. Results and discussion

This survey was part of a larger study assessing the effects of reduced-impact logging on bird community composition and abundance. The list should be of benefit to other researchers assessing disturbance associated responses of Neotropical avifauna, and to facilitate increased understanding of the diverse bird assemblages found within the lowland subtropical forests of Bolivia. During point count surveys, we identified approximately 5 050 birds, belonging to 155 species, and 33 families (see Table 1).

Outside of the survey period, several species were noted in addition to those accounted for within the forested areas of the concession. These included the harpy eagle (*Harpia harpyja*), crested eagle (*Morphnus guianensis*), great razor-billed curassow (*Mitu tuberosa*), bare-faced curassow (Crax fasciolata), ferruginous pygmy-owl (*Glaucidium brasilianum*), common potoo (*Nyctibius griseus*), pauraque (*Nyctidromus albicollis*) and bare-necked fruitcrow (*Querula purpurata*).

Although avian species richness was nearly identical between the harvested and unharvested areas of the concession (unlogged 133; logged 132), this result obscures underlying differences in species composition. Our results suggest that the avian families Ramphastidae, Falconidae and Formicariidae may be adversely affected by the logging activities in this forest. At the species level, concern may be warranted regarding the absence of the Barred-forest falcon and lower abundance of the Red-necked Woodpecker, Channel-billed Toucan, Red-billed Toucan, Black-faced Antthrush, Spot-backed Antbird, and Gray-fronted dove within the harvested areas of the concession. In contrast, the Black-throated Antbird, Yellow-tufted Woodpecker, Buff-throated Saltator, and Moustached Wren, appear to be currently benefiting from logging associated disturbance.

Due to temporal and seasonal variation in bird species vocalization and presence, results should be interpreted acknowledging the season of the survey and the time of day during which the surveys were carried out. It should also be acknowledged that the mere presence of a species in an area does not necessarily mean that the area possessed suitable habitat for that species’ long-term persistence (O'Brien et al., 2003). At the time of the survey, the first logging rotation for the concession was not as yet completed, and disturbance processes associated with selective logging activity occurred from only one to four years previously. This temporal period of disturbance is well short of that by which most localized avian extinctions are predicted to occur following anthropogenic disturbance processes (Robinson 1999; Mason & Thiollay 2001).

Table 4.1. Bird species encountered during bird surveys conducted from December 2003 to February 2004 within 360 sampling points equally distributed between the harvested (Log) and unharvested (Unl) blocks of the reduced-impact logged La Chonta concession, Department of Santa Cruz, Bolivia. Bird abundance is grouped according to the number of total contacts made during the survey within the harvested and unharvested areas. Birds are labeled either as abundant (ab; >99), common (com; >29), uncommon (unc; 9>n<30), rare (rar; 2>n<10), present (pre; 1,2), or not observed (- ; 0).

Scientific name	Common name	Unl	Log
Tinamidae			
Crypturellus soui	Little Tinamou	unc	unc
Crypturellus cinereous	Cinereous Tinamou	unc	unc
Crypturellus strigulosus	Brazilian Tinamou	rar	unc
Crypturellus tataupa	Tatapua Tinamou	rar	pre
Crypturellus undulatus	Undulated Tinamou	com	com
Tinamous tao	Gray Tinamou	pre	pre
Cathartidae			
Sarcoramphus papa	King Vulture	-	pre
Accipitridae			
Spizaetus ornatus	Ornate Hawk-eagle	pre	pre
Spizaetus tyrannus	Black Hawk-eagle	pre	-
Falconidae			
Micrastur ruficollis	Barred Forest-falcon	rar	-
Falco rufigularis	Bat Falcon	pre	-
Micrastur gilvicollis	Lined Forest-falcon	pre	-
Micrastur semitorquatus	Collared Forest-falcon	pre	-
Cracidae			
Penelope jaquacu	Spix's Guan	rar	rar
Pipile pipile	Blue-Throated Piping-guan	pre	pre
Columbidae			
Columba speciosa	Scaled Pigeon	unc	com
Columba plumbea	Plumbeous Pigeon	unc	unc
Columbia subvinacea	Ruddy Pigeon	com	com
Claravis pretiosa	Blue Ground-dove	com	com
Geotrygon montana	Ruddy Quail-dove	rar	pre
Leptotila rufaxilla	Gray-fronted dove	com	unc
Psittacidae			

Brotogeris cyanoptera	Cobalt-winged Parakeet	unc	com
Pyrrhura molinae	Green-cheeked Parakeet	unc	unc
Pionus menstruus	Blue-headed Parrot	unc	unc
Ara severa	Chestnut-fronted Macaw	rar	unc
Ara chloroptera	Red and Green Macaw	rar	unc
Ara arauna	Blue and Yellow Macaw	rar	rar
Aratinga leucophthalmus	White-eyed Parakeet	-	pre
Amazona farinosa	Mealy Parrot	com	com
Cuculidae			
Piaya cayana	Squirrel Cuckoo	unc	unc
Tapera naevia	Striped Cuckoo	pre	-
Coccyzus americanus	Yellow-billed Cuckoo	-	pre
Strigidae			
Otus watsonii	Tawny-bellied Screech-owl	pre	rar
Ciccaba huhula	Black-banded owl	pre	-
Carpimulgidae			
Nyctiphrynus ocellatus	Ocellated Poorwill	rar	unc
Trochilidae			
Phaethornis ruber	Reddish Hermit	unc	unc
Thalurania furcata	Fork-tailed Woodnymph	rar	pre
Phaethornis hispidus	White-bearded Hermit	rar	-
Heliothryx barroti	Purple-crowned Fairy	pre	pre
Glaucis hirsuta	Rufous-breasted Hermit	pre	-
Hylocharis cyanus	White-chinned Sapphire	com	rar
Trogonidae			
Trogon curucui	Blue-crowned Trogon	unc	unc
Trogon collaris	Collared Trogon	com	com
Trogon melanurus	Black-tailed Trogon	com	com
Motmotidae			
Motmotus motmota	Blue-crowned Motmot	unc	com
Bucconidae			
Monasa morphoeus	White-fronted Nunbird	unc	unc
Nonnula ruficapilla	Gray-cheeked Nunlet	rar	rar
Nystalus striolatus	Striolated Puffbird	rar	rar
Notharcus macrohynchos	White-necked Puffbird	-	rar
Monasa nigrifrons	Black-fronted Nunbird	com	com
Galbulidae			

Galbula ruficauda	Rufous-tailed Jacamar	pre	pre
Brachygalba lugubris	Brown Jacamar	-	pre
Ramphastidae			
Pteroglossus castanotis	Chestnut-eared Aracari	rar	rar
Ramphastos tucanus	Red-billed Toucan	com	unc
Rhamphastos vitellinus	Channel-billed Toucan	com	unc
Picidae			
Melanerpes cruentatus	Yellow-tufted Woodpecker	unc	com
Campephilus rubricollis	Red-necked Woodpecker	unc	rar
Piculus leucolaemus	White-throated Woodpecker	rar	pre
Celeus torquatus	Ringed Woodpecker	pre	rar
Picumnus aurifrons	Bar-breasted Piculet	pre	-
Dendrocolaptidae			
Dendrexetastes certhia	Cinnamon-throated W’creeper	unc	unc
Lepidocolaptes albolineatus	Lineated Woodcreeper	rar	rar
Sittasomus griseicapillus	Olivaceous Woodcreeper	rar	rar
Dendrocolaptes certhia	Barred Woodcreeper	rar	pre
Dendrocolaptes piccumnus	Black-banded Woodcreeper	pre	pre
Nasica longirostris	Long-billed Woodcreeper	pre	pre
Dendrocincla fuliginosa	Plain-brown Woodcreeper	pre	-
Xiphorhyncus guttatus	Buff-throated Woodcreeper	com	com
Furnariidae			
Automolus ochrolaemus	Buff-throated Foliage-Gleaner	unc	unc
Xenops rutilans	Streaked Xenops	rar	pre
Formicariidae			
Hylopezus berlepschi	Amazonian Antpitta	-	pre
Formicarius analis	Black-faced Antthrush	com	unc
Myrmeciza atrothorax	Black-throated Antbird	unc	com
Thamnophilus amazonicus	Amazonian Antshrike	unc	unc
Hylophylax naevius	Spot-backed Antbird	unc	rar
Myrmotherula axillaris	White-flanked Antwren	rar	rar
Thamnophilus sticturus	Bolivian-slaty Antshrike	rar	rar
Hylophylax poecilonota	Scale-backed Antbird	rar	rar
Pyriglena leuconota	White-backed Fire-eye	pre	rar
Phlegopsis nigromaculata	Black-spotted Bare-eye	pre	pre
Hypocnemoides maculicauda	Band-tailed Antbird	pre	-
Myrmeciza hemimelaena	Chestnut-tailed Antbird	com	com

Thamnophilus palliatus	Chestnut-backed Antshrike	com	com
Dysithamnus mentalis	Plain Antvireo	com	com
Herpsilochmus rufimarginatus	Rufous-winged Antwren	ab	ab
Thamnophilus schistaceus	Plain-winged Antshrike	ab	ab
Cercomacra cinerascens	Gray Antbird	ab	ab
Hypocnemis cantator	Warbling Antbird	ab	com
Tyrannidae			
Myiarchus tuberculifer	Dusky-capped Flycatcher	unc	com
Tolmomyias assimilis	Yellow-margined Flycatcher	unc	unc
Hemitriccus flammulatus	Flammulated Bamboo-Tyrant	unc	unc
Attila spadiceus	Bright-rumped Attila	unc	unc
Rhytipterna simplex	Grayish Mourner	unc	unc
Myiornis ecaudatus	Short-tailed Pygmy-Tyrant	rar	unc
Legatus leucophaeus	Piratic Flycatcher	rar	rar
Tolmomyias sulphurescens	Yellow-olive Flycatcher	rar	rar
Hemitriccus minor	Snethlage's Tody-tyrant	rar	pre
Ramphotrigon ruficauda	Rufous-tailed Flatbill	rar	-
Onychorhynchus coronatus	Amazonian Royal Flycatcher	pre	rar
Lathrotriccus euleri	Euler's Flycatcher	pre	pre
Casiornis rufa	Rufous Casiornis	pre	-
Myiodynastes maculatus	Streaked Flycatcher	pre	-
Tityra cayana	Black-tailed Tityra	pre	-
Attila bolivianus	White-eyed Attila	-	pre
Leptopogon amaurocephalus	Sepia-capped Flycatcher	-	pre
Pachyramphus marginatus	Black-capped Becard	-	pre
Pachyramphus minor	Pink-throated Becard	-	pre
Pachyramphus polychopterus	White-winged Becard	-	pre
Tyrannus melancholicus	Tropical Kingbird	-	pre
Myiopagis gaimardi	Forest Elaenia	com	com
Corythopis torquata	Ringed Antpipit	com	unc
Cotingidae			
Laniocera hypopyrra	Cinereous Mourner	rar	rar
Cephalopterus ornatus	Amazonian Umbrellabird	-	pre
Lipaugus vociferans	Screaming Piha	ab	ab
Pipridae			
Machaeropterus pyrocephalus	Fiery-capped Manakin	unc	unc
Neopelma sulphureiventer	Sulphur-bellied Tyrant-Manakin	unc	unc

Piprites chloris	Wing-barred Piprites	rar	pre
Pipra fasciicauda	Band-tailed Manakin	pre	pre
Pipra rubrocapilla	Red-headed Manakin	pre	-
Troglodytidae			
Thryothorus genibarbis	Moustached Wren	unc	unc
Thryothorus guarayanus	Fawn-breasted Wren	rar	rar
Campylorhynchus turdinus	Thrush-like Wren	-	pre
Microcerculus marginatus	Scaly-breasted Wren	-	pre
Sylviinae			
Ramphocaenus melanurus	Long-billed gnatwren	com	unc
Turdinae			
Turdus albicollis	White-necked Thrush	unc	unc
Turdus amaurochalinus	Creamy-bellied Thrush	pre	pre
Turdus hauxwelli	Hauxwell's Thrush	-	pre
Vireonidae			
Cyclarhis gujanensis	Rufous-browed Peppershrike	rar	unc
Hylophilus pectoralis	Ashy-headed Greenlet	pre	pre
Hylophilus muscicapinus	Buff-cheeked Greenlet	com	com
Emberizinae			
Arremon taciturnus	Pectoral Sparrow	rar	rar
Cardinalinae			
Cyanocompsa cyanoides	Blue-black Grosbeak	unc	unc
Saltator maximus	Buff-throated Saltator	-	rar
Thraupinae			
Tangara chilensis	Paradise Tanager	unc	unc
Hemithraupis guira	Guira Tanager	rar	pre
Euphonia rufiventris	Rufous-bellied Euphonia	pre	rar
Euphonia cyanocephala	Golden-rumped Euphonia	pre	pre
Euphonia chrysopasta	White-lored Euphonia	pre	-
Tachyphonus luctuosus	White-shouldered Tanager	pre	-
Euphonia laniirostris	Thick-billed Euphonia	pre	-
Euphonia xanthogaster	Orange-bellied Euphonia	pre	-
Tachyphonus cristatus	flame-crested Tanager	pre	-
Ramphocelus carbo	Silver-beaked Tanager	-	rar
Dacnis cayana	Blue Dacnis	-	pre
Eucometis penicillata	Gray-headed Tanager	-	pre
Thraupis sayaca	Sayaca Tanager	-	pre

Thraupis palmarum	Palm Tanager	-	pre
Habia rubica	Red-crowned Ant-tanager	com	com
Coereba flaveola	Bananaquit	rar	rar
Parulidae			
Basileuterus culicivorus	Golden-crowned Warbler	unc	com
Parula pitiayumi	Tropical Parula	rar	rar
Icteridae			
Psarocolius decumanus	Crested Oropendola	rar	pre
Psarocolius bifasciatus	Olive Oropendola	rar	-
Cacicus cela	Yellow-rumped Cacique	-	pre

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Photo by Annika Felton

Channel-billed toucan (*Ramphastos vitellinus*)

Chapter 5

BIRD COMMUNITY RESPONSES TO REDUCED-IMPACT LOGGING IN A CERTIFIED FORESTRY CONCESSION IN LOWLAND BOLIVIA

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5.1. Abstract

We studied bird community composition and abundance within the logged and unlogged forest areas of a certified forestry concession in lowland Bolivia. The logged forest was harvested using reduced-impact logging techniques between one and four years previously. We used canonical correspondence analysis to describe the relationship between selected environmental variables and bird species abundance data, and the Indicator Value procedure to test for associations between bird species and the logged and unlogged habitats. Approximately one-third of birds were restricted to either the logged or unlogged areas, with twenty percent of all species only encountered in, or significantly more abundant in, the unlogged areas of the concession. The majority of birds found in significantly higher abundance in the unlogged areas of the concession were associated with forest habitats dominated by large trees, or a high diversity of trees, providing dense canopy cover and deep leaf litter, with an understorey dominated by ferns. Over forty percent of bird species that were significantly associated with the unlogged areas of the concession are of conservation concern. In contrast, the majority of birds associated with the logged areas of the concession are known to be relatively resilient to human disturbance. The majority of species which exhibited significant lower abundances in the logged areas of the concession belonged to insectivorous or frugivorous feeding guilds. We discuss whether current management practices within this certified concession are sustainable and how our results can be used to guide future research and inform better practice.

5.2. Introduction

Due to accelerating rates of global biodiversity loss, attempts are being made to focus conservation actions on those ecosystems under greatest threat and possessing a disproportionate share of the world's biodiversity (Myers et al., 2000; Sala et al., 2000). Up to two-thirds of the world's terrestrial species are found in tropical forests (Groombridge & Jenkins 2002), that are being degraded at a rate of fifteen million hectares per year (FAO 2001). Therefore, preservation of tropical forest ecosystems will be an integral component of successful global conservation efforts. As insufficient area of tropical forest can be included in protected areas to halt loss of biodiversity (Soulé & Sanjayan 1998), conservation efforts have shifted towards the adoption of land-uses outside of parks that are considered compatible with the maintenance of forest biodiversity (Frumhoff & Losos 1998; Putz et al., 2001).

Selective logging is the dominant form of timber extraction in the tropics, and is considered to be one of the land-uses that can reconcile human demands for resources with the need to maintain biodiversity (Rametsteiner & Simula 2003). Selective logging involves the periodic extraction of commercially valuable tree species from forests (Johns 1988b). The largest remaining tracts of tropical forest occur in Latin America (FAO 2001), and by the mid-1990s an estimated 28% of these forests had been subjected to selective logging (Grieser Johns 1997; Asner et al., 2005). The extent to which selective logging degrades forest structure varies considerably, depending on extraction rates and the extent of collateral damage to the residual stand (Johns 1988a). As a silvicultural system, selective logging therefore represents a continuum of anthropogenic disturbance, which at one extreme may be virtually synonymous with deforestation, or at the other extreme may allow for the retention of much of a forest's canopy and vegetation structure (van Soest 1998). It is expected that somewhere along this continuum, selective logging procedures can be developed that successfully combine economically viable levels of timber extraction with biodiversity conservation (Pinard & Putz 1996a).

Reduced-impact logging (RIL) is a modified form of selective logging that is increasingly employed in tropical forests. It incorporates a variety of techniques aimed at lowering levels of damage to the residual stand (Putz et al., 2001). These include directional felling, pre-harvest vine cutting, and preliminary inventories to reduce the number and density of logging roads (Heinrich 1995). Recent studies suggest that reduced-impact logging of tropical forests causes less damage to forest structure than conventional selective logging techniques (Asner et al., 2004a; Huth et al., 2004). However, reduced-impact logging is still a form of commercial forestry that increases the frequency and extent of canopy discontinuities (Jackson et al., 2002). These changes to vegetation structure can alter microclimatic conditions, including temperature, wind and humidity levels (Pinard & Cropper 2000; Asner et al., 2004b). The capacity of these forests to retain their original complement of biodiversity is not well known (Bojanic & Bulte 2002; Dauber et al., 2005).

Birds are an ideal taxon for assessing the impacts of logging on biodiversity in tropical forests, as bird community composition can be strongly influenced by disturbance to forest vegetation structure (Wiens 1992; Mason & Thiollay 2001; Barlow & Peres 2004). Birds also perform vital ecological functions in tropical forests and have roles as pollinators, seed dispersers, and predators (Stiles 1983). Furthermore, quantitative assessment of the IUCN red list shows that the threat status of the world's birds has steadily worsened since 1988 (Butchart et al., 2004), with 93% of threatened forest avifauna found in tropical forests (Birdlife-International 2004).

Studies of conventional selective logging suggest that disturbance to vegetation structure and microclimate affects bird species in a variety of ways, and is highly dependent on the guild being considered (Mason 1996; Woltmann 2003; Wunderle et al., 2006). For instance, because reproductive activity in understorey plants is positively correlated with increased irradiance (Costa & Magnusson 2003), members of some avian guilds (eg. frugivores, nectarivores) can increase in abundance following selective logging due to the increased availability of nectar and fruit in areas of canopy discontinuity (Mason 1996; Wunderle et al., 2006). In contrast, understorey insectivores are particularly susceptible to disturbance associated with selective logging (Mason & Thiollay 2001; Sekercioglu et al., 2002; Sodhi et al., 2004; Barlow et al., 2006; Barlow et al., 2007; Gray et al., 2007). Members of this guild may be physiologically intolerant to increased variation in temperature and humidity levels associated with decreased canopy continuity (Karr & Brawn 1990; Mason 1996; Sekercioglu et al., 2002; Barlow & Peres 2004). Each species may react differently to a given forest disturbance depending (in part) on its foraging behavior, habitat specialization, and physiological sensitivity to microclimatic changes (Thiollay 1992; Sekercioglu et al., 2002). For these reasons, studies of bird species' responses to tropical forest disturbance have reported negative or positive impacts depending on the extent of disturbance, and the species pool being considered (Hill & Hamer 2004).

There are over 1 400 species of bird known from Bolivia, with the majority of species found in the sub-tropical and tropical forests of the lowlands (Pacheco 1998). Almost half of these areas are now granted to forestry concessions (Mostacedo & Fredericksen 1999). In 1996, a new forestry law was enacted to promote the sustainable harvesting of timber (Mostacedo and Fredericksen, 1999). To achieve best-management practices, reduced-impact logging techniques have gained widespread application in Bolivia and, as of 2005, concessions covering over 2.2 million hectares had obtained certification by the Forest Stewardship Council (FSC, 2005).

We suggest that there is a need to evaluate the compatibility of reduced-impact logging with biodiversity maintenance. In this paper, we use a reduced-impact logged sub-tropical forest in Santa Cruz province, lowland Bolivia, as a case study to examine; (i) differences in avian diversity and community composition in logged and unlogged forests; and (ii) the potential conservation related repercussions of any observed differences.

5.3. Methods

5.3.1. Site description

Our study area was located in the subtropical humid forest of the Guarayos Forest Reserve, Departmento Santa Cruz, Bolivia. Research was conducted in the 100 000 ha forestry concession "La Chonta". This is owned and managed by Agroindustria

Forestal La Chonta (509000 to 545000 easting, 8275500 to 824900 northing; Figure 1.). The forest has an average elevation of 320 m (range 230-390m). The soils consist of oxisols, ultisols, and inceptisols (Park et al., 2005). The mean annual temperature is 25° C with a mean annual precipitation of approximately 1 560 mm. The region experiences a distinct dry season from May to October. The entire concession was subjected to legal and illegal selective logging of mahogany (*Swietenia macrophylla*), and spanish cedar (*Cedrela odorata*) 10 – 25 years prior to this study. The concession was certified by SmartWood in 1998.

5.3.2. Harvesting procedure

Approximately 2 500 ha is harvested annually over three contiguous 850 ha blocks (~4 km x 2 km), yielding 50 000 m^3 of timber. Eighteen commercial tree species were harvested during the time of this study (2003-2004) including *Ficus boliviana*, *Hura crepitans*, *Terminalia oblonga*, *Pseudolmedia laevis*, *Cariana ianeirensis*, and *C. estrellensis*. Average harvest intensity in this forest is approximately 4 trees/ha (Jackson et al., 2002). The forestry company Agroindustria Forestal La Chonta conducts inventories of harvestable trees one year prior to logging. The minimum size for harvest is 50 cm diameter at breast-height (dbh) for all species except *F. boliviensis* and *H. crepitans*, which are harvested above 70 cm dbh. One in five harvestable trees is required by law to be left as a seed tree. During pre-harvesting inventory, trees selected for felling are cleared of all vines around the bole.

The forestry company uses a ‘fishbone’ harvesting strategy with a single primary north-south road bisecting each 850 ha block. Skid trails are located 100-150 m apart and run in an east-west direction on either side of the primary road. Chainsaw teams trained in directional felling techniques try to reduce damage to the residual stand during felling. Removal and loading of boles is conducted using rubber-tired skidders to reduce soil compaction. It is intended that blocks be re-cut in 25 to 30 years.

5.3.3. Survey design

Logging blocks were harvested systematically in the La Chonta concession (see Figure A2.2). Logging related disturbance was adjacent to, but south and west of, our unlogged control blocks. We therefore acknowledge the theoretical possibility that any observed differences between bird communities found within the harvested and unharvested blocks of the concession, could be the product of a priori spatial variation in vegetation. However, unlogged areas of the concession were destined to be logged shortly after completion of our research. As such, their “unlogged” status was not indicative of associated differences in vegetation type. Second, tree species composition and abundance was consistent between the unharvested areas of the residual stand and the unlogged forest (A. Felton unpublished data). Third, a stratified-random sampling design was used which incorporated commercial tree species occurrence, vegetation height, and disturbance type. This design increased the likelihood that logged and unlogged survey points were appropriate for comparison, and accounted for natural variation in vegetation structure. This experimental design also addressed the concern that selective logging disproportionately disturbs forest with commercial densities of harvestable trees, and any random placement of survey points within the harvested blocks was unlikely to sample habitat directly comparable to that found within the unlogged forest blocks.

We defined five habitat categories: 1. ‘target’ points (T) with vegetation height over 20 m and possessing one of five commercial tree species (*Ficus boliviensis*, *Hura crepitans*, *Cariniana estrellensis*, *C. ianeirensis*, *Terminalia oblonga*) of harvestable size; 2. ‘future’ points (F) from 12-20 m in height and possessing a commercial tree of the afore mentioned five species not yet of harvestable size but above 30 cm dbh; 3. ‘non-target’ points (N) of less than 12m in height and not possessing commercial trees above 10 cm dbh; 4. ‘gap’ points (G) possessing a tree-fall gap caused by the felling of a tree (in the harvested blocks) or a natural tree fall (in the unlogged blocks) of greater than 50 cm dbh; and 5. ‘road’ points (R) located on a primary north-south logging road in the logged forest, or along the main north-south access path in the unlogged forest.

In each logging block, one to two clusters of 15 survey points, representing three of each of the five habitat categories, were randomly chosen from available alternatives (as identified during preliminary vegetation surveys) and located along three ~1 km long transects (see Figure A2.2).We placed survey points at least 300 m apart and at leat 500 m from the edge of neighbouring treatment blocks. This design was repeated until 180 survey points were designated for the logged area. The equivalent survey design was repeated in the unlogged forest for the total of 360 survey points used in the study. In the logged forest, the ‘target’ category was represented by seed trees left by loggers to aid regeneration. Trees not harvested due to undesirability (eg. insufficient bole length or malformation) were not included in this category. In the residual stand of the logged forest, ‘target’, ‘non-target’, and ‘future’ points were located at least 15 m away from skid trails or logging gaps. All habitat categories (other than ‘road’ points) were located at least 250 m from logging roads.

5.3.4. Measurement of vegetation structure and floristics

We conducted vegetation structure and floristic surveys during June and July 2004 within the 360 survey points. To reduce the effects of seasonal variation, logged and unlogged areas were surveyed on alternate days, as were blocks logged in different years. At each survey point, we marked a 20 m x 20 m quadrat within which all trees, palms, poles and snags were counted if part of their bole encroached on the quadrat. Trees (>10 cm dbh) were identified to species-level by botanists from the Instituto Boliviano de Investigación Forestal (IBIF). We defined poles as trees less than 10 cm dbh but taller than 3 m. We counted palms up to 3 m in height were, with palms over this height also identified to species. We also took three measurements of vegetation structure from four equidistant markers located 7 m from the quadrat center. We used a 2 m rope held vertically and marked at 10 cm intervals to assess understorey density of vegetation, we. We held the rope in the centre of the quadrat with the number of bands visible from each of the four markers counted by the observer which provided our index of understorey density. We measured canopy height at each marker using a clinometer and a laser rangefinder. We also quantified canopy cover at each marker using a densiometer.

We defined a 2 x 2 m plot at each of the four markers. In each plot, we estimated the percentage cover of grasses, ferns, palms, seedlings, dead wood, dirt, rock, sand, *Erythrochiton fallax* (Rutaceae), *Heliconia* spp. (Heliconiaceae), other herbs, and vines. Vine coverage was divided into two classes: 0-1 m (“vine low”) and 1-2 m above ground (“vine high”). For further details of vegetation surveys see Felton et al. (2006b).

5.3.5. Bird surveys

We used the point-count method of surveying bird species abundance at each of the 360 survey points. Distance to individual birds from the observer (A.F.) was grouped into two radius intervals: 0-20 m and 20 m to infinity (as per Bibby et al., 2000). We conducted surveys from December to February of the 2003-2004 wet season. We began surveys at first light (5:45-6:00 am), and continued until approximately 10:30 am. This period overlapped with the daily peak in bird vocal activity. A day’s survey consisted of visiting three points of each of the five habitat types (15 points in total). Each point was surveyed for 12 minutes. We included birds flushed from the survey point on approach by the observer, while birds flying over the survey area were not included in the analysis. We only undertook surveys if the weather was fine (eg. no rain or high wind).

Due to the density of forest vegetation, most identifications were made acoustically, rather than visually. When there was potential for confusion regarding the number of calling individuals, the most conservative option was used. Recordings were made using a Sony TCM 5000 tape-recorder attached to a Sennheiser ME66 microphone. These recordings were used as a supplement to in-the-field identification of vocalizing species. For species that we were unable to identify in the field, symbolic representations of songs were noted, in addition to notes on the recording time, direction, and estimated distance to the call. This enabled us to match subsequent identifications with abundance and distance information. Unknown recordings were identified using the CD-ROM Birds of Bolivia, 2.0 (Mayer 2000), or by an expert (B.H). We used survey results as a crude surrogate of relative abundance, rather than as estimates of absolute density.

5.3.5. Statistical analysis

We assessed the thoroughness of our bird sampling in the logged and unlogged forests using sample-based rarefaction curves constructed with the Mao Tau function in EstimateS v.8 (Colwell 2005). We used the Indicator Value (IndVal) procedure (Dufrêne & Legendre 1997) to test associations between individual bird species and the logged and unlogged areas of the concession. Higher Indicator Values therefore indicate species which are more representative for the given habitat. A random reallocation procedure using 1000 iterations was conducted to test the significant level of IndVal results (alpha=0.05).

We used canonical correspondence analysis (CCA ter Braak 1986) to describe the relationship between selected environmental variables and bird data (0-20 m). CCA is a multivariate ordination technique that uses information on species' abundances at sites and the environmental variables at those sites, to produce an ordination of species distributions using nonlinear, unimodal responses (Wiens et al., 2001; Gunnarsson et al., 2006). CCA is especially useful for analyzing species-environment relationships (Palmer 1993; Hobson et al., 2000; Grand & Cushman 2003). All analyses were carried out using the ADE4 software package available online within the statistical analysis software R. As our vegetation structure measurements were undertaken within areas of 20 x 20 m, the usefulness of CCA in our study diminishes for species with individual distributions influenced by structural and floristic variables operating at larger spatial scales (see Felton et al., 2008).

5.4. Results

During point count surveys, we identified 5 062 birds, belonging to 158 species, and 35 families. For a complete list of all species found during this study within the La Chonta concession and their relative abundance see Felton et al. (2007). In the unlogged forest 133 species were identified, of which 27 species were not found in the logged forest. In the logged forest, 132 species were identified, of which 24 species were not found in the unlogged forest. The results of sample-based rarefaction curves (Figure 5.3) indicate that our sampling efforts were sufficient due to their rapid approach to asymptote.

We present the IndVal scores to indicate the relative contribution of bird species to the established differences in bird community composition between the logged and unlogged areas (Table 5.1; Table 5.2). Random reallocation permutations demonstrated that 9 bird species were significantly associated with the unlogged areas of the concession (Table 5.1), whereas 7 bird species were significantly associated with the logged areas (Table 5.2). Bird species considered to exhibit a 'high' sensitivity to disturbance (Stotz et al., 1996), were prevalent amongst those species significantly associated with the unlogged areas (40% of species), and absent amongst species significantly associated with the logged areas (Table 5.1, 5.2). Birds belonging to the insectivorous or frugivorous feeding guilds were more likely to be significantly associated with the unlogged areas than the logged areas (Table 5.1, 5.2). The only granivore that demonstrated a significant difference between the disturbed and undisturbed areas was primarily associated with logged areas of the concession (Table 5.2). The four forest-falcon species, barred forest-falcon (*Micrastur ruficollis*), collared forest-falcon (*Micrastur semitorquatus*), lined forest-falcon (*Micrastur gilvicollis*), and bat falcon (*Falco rufigularis*), were observed only in unlogged sites.

Vegetation structure variables differed in their relationship to the first and second axes of the CCA ordination (Figure 5.4). The first canonical axis (eigenvalue = 0.11) distinguished between sites with more trees, greater tree diversity, closed canopy, low vines, and deeper leaf litter in the positive direction, from those with more disturbed ground (dirt) and coverage by ferns, *Heliconia* spp., and palms in the negative direction. Unlogged habitat categories primarily had positive scores on the first canonical axis, with logged sites possessing positive scores (Figure 5.4).

The second canonical axis (eigenvalue = 0.095) primarily described changes in openness of the understorey and associated differences in the dominance of different understorey vegetation types (Figure 5.4). Along this second axis, sites dominated by seedlings and low vines in the negative direction were distinguished from sites dominated by ferns and trees in the positive direction. Habitat categories associated with logging disturbance were situated along the negative aspect of the second canonical axis, with unlogged categories located along the positive axis (Figure 5.4).

Bird species found in significantly higher abundance in the unlogged area were primarily distributed positively along the first and second canonical axis (Figure 5.5). The bird species recorded at significantly higher abundance in the logged area were primarily associated with negative scores on the first canonical axis and consistently associated with negative scores on the second canonical axis (Figure 5.6).

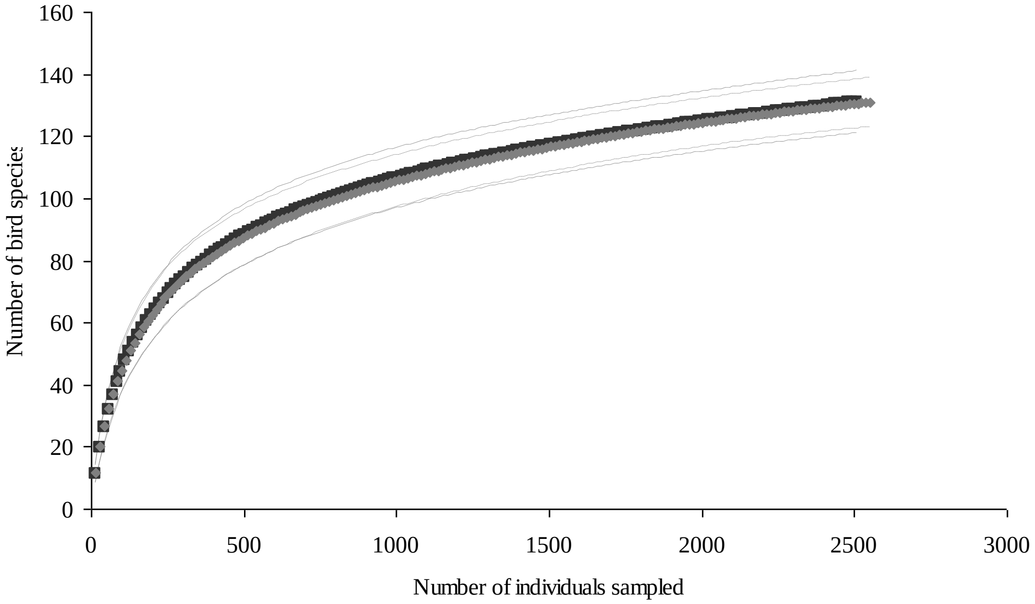

Figure 5.3. Sample-based rarefaction curves calculated using Mao Tau as per Colwell (2005) for unlogged and logged forest points within the La Chonta concession Bolivia. The squares (unlogged) and diamonds (logged) represent individual point count results used for the accumulation curve and the dashed lines are the 95% confidence intervals. The x-axis is scaled to show the number of individuals encountered.

Table 5.1. The twenty bird species with the highest Indicator Value (IV) for unlogged habitats, representing the degree to which a given species is associated with unlogged (U) versus logged (L) areas in the La Chonta concession, Department of Santa Cruz, Bolivia. A random reallocation procedure using 1000 iterations was conducted to test the significant level of IndVal results (alpha=0.05). The number of observations for a given species in unlogged or logged surveys is also presented. “Sensitivity” to disturbance ratings are low (L), medium (M) and high (H), as per Stotz et al. (1996).

Family	Common name	Scientific name	Unlogged	Logged	IV	P value	Sensitivity	Foraging guild
Formicariidae	black-faced antthrush	*Formicarius analis*	33	14	11.31	0.003	M	Terrestrial insectivore
Falconidae	barred forest-falcon	*Micrastur ruficollis*	9	0	5	0.004	M	Raptor
Picidae	red-necked woodpecker	*Campephilus rubricollis*	27	8	9.86	0.004	H	Bark insectivore
Ramphastidae	channel-billed toucan	*Rhamphastos vitellinus*	34	13	9.24	0.005	H	Frugivore/ omnivore
Columbia	gray-fronted dove	*Leptotilla rufaxilla*	49	28	13.79	0.02	M	Frugivore
Thamnophilidae	spot-backed antbird	*Hylophylax naevia*	18	6	5.83	0.02	H	Gleaning insectivore
Thraupinae	Guira tanager	*Hemithraupis guira*	8	1	11.96	0.02	L	Gleaning insectivore
Ramphastidae	red-billed toucan	*Ramphastos tucanus*	41	18	9.65	0.02	H	Frugivore
Polioptilidae	long-billed gnatwren	*Ramphocaenus melanurus*	38	22	11.96	0.02	L	Gleaning insectivore

Table 5.2. The twenty bird species with the highest Indicator Value (IV) for logged habitats, representing the degree to which a given species is associated with logged (U) versus unlogged (L) areas in the La Chonta concession, Department of Santa Cruz, Bolivia. A random reallocation procedure using 1000 iterations was conducted to test the significant level of IndVal results (alpha=0.05). The number of observations for a given species in logged or unlogged surveys is also presented. "Sensitivity" to disturbance ratings are low (L), medium (M) and high (H), as per Stotz et al. (1996).

Family	Common name	Scientific name	Logged	Unlogged	IV	P value	Sensitivity	Foraging guild
Thamnophilidae	black-throated antbird	*Myrmeciza atrothorax*	39	10	14.15	0.0001	L	Gleaning insectivore
Tinamidae	little tinamou	*Crypturellus soui*	26	13	8.15	0.03	L	Terrestrial granivore
Parulinae	golden-crowned warbler	*Basileuterus culicivorus*	36	21	12.28	0.01	M	Insectivore/omnivore
Picidae	yellow-tufted woodpecker	*Melanerpes cruentatus*	35	12	12.83	0.002	L	Arboreal omnivore
Cardinalinae	buff-throated saltator	*Saltator maximus*	9	0	5	0.003	L	Arboreal omnivore
Troglodytidae	moutached wren	*Thryothorus genibarbis*	29	15	9.15	0.03	L	Gleaning insectivore
Columbidae	Scaled pigeon	*Columba speciosa*	39	26	12.67	0.036	M	Frugivore

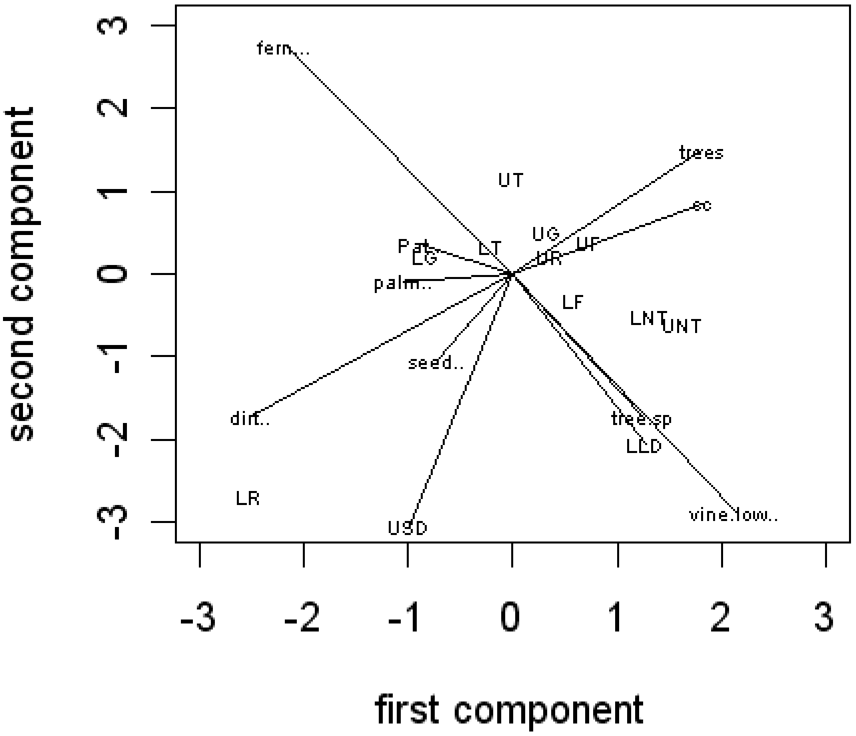

Figure. 5.4. Plot scores (linear combination of variable scores) for the first two axes of canonical scores from CCA analysis for vegetation variables and habitat categories in the logged and unlogged forest of the La Chonta Concession Bolivia.

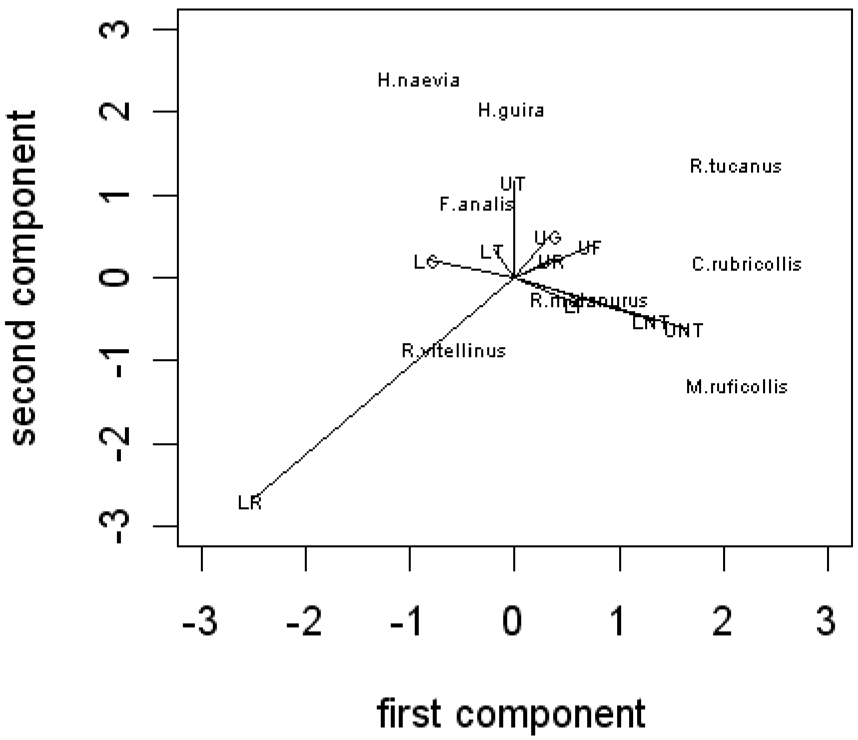

Figure. 5.5. Average scores are presented for bird species in the first two axes of the CCA analysis. Only those bird species that were significantly associated with the unlogged areas of the La Chonta Concession Bolivia as determined using the IndVal technique are shown. See Table 5.1for details relating to the bird species represented.

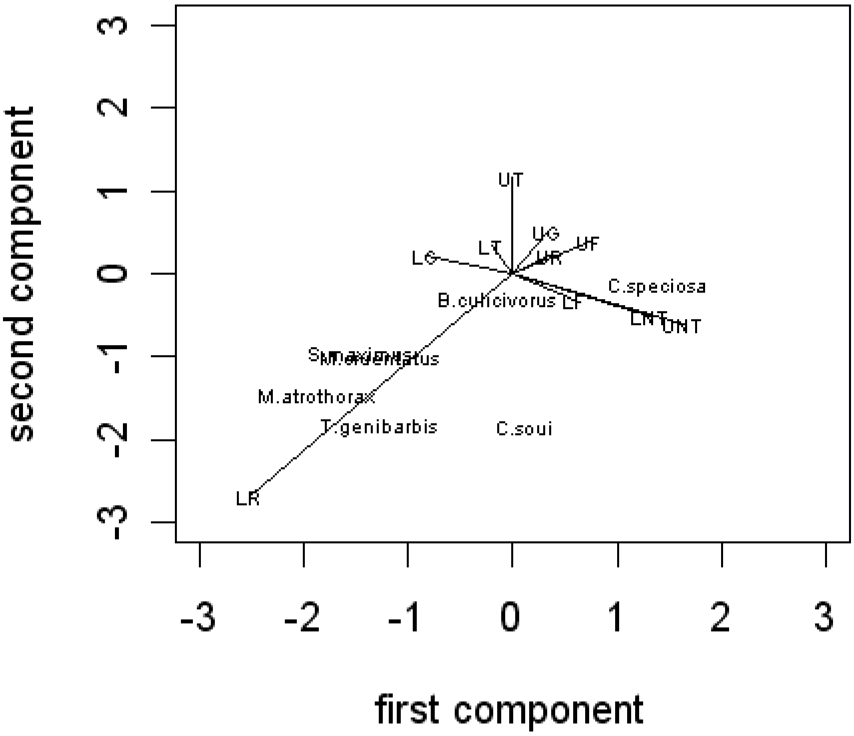

Figure. 5.6. . Average scores are presented for bird species in the first two axes of the CCA analysis. Only those bird species that were significantly associated with the logged areas of the La Chonta Concession Bolivia as determined using the IndVal technique are shown. See Table 5.2 for details relating to the bird species represented.

5.5. Discussion

We found that bird communities significantly differed in composition between the logged and unlogged areas of the La Chonta concession. Approximately 20% of species were exclusive to or significantly more abundant in the unlogged areas. Furthermore, over 40% of bird species that exhibited a significant association with the unlogged area (Table 1) are considered to be highly sensitive to human disturbance, and of conservation concern (Stotz et al., 1996). In contrast, those species which were significantly associated with the logged areas (Table 2) are primarily species that are known to be relatively resilient to human disturbance (Thiollay 1992; Canaday 1996; Stotz et al., 1996; Marsden et al., 2001). Recently Gray et al. (2007) analyzed the results of 57 published studies of avian feeding guild responses to tropical forest disturbance and determined that the abundance of avian granivores tends to increase significantly, whereas insectivores and frugivores tend to decrease significantly. Our findings are consistent with their results. We suggest that despite the employment of reduced impact logging procedures and the awarding of certification status to this concession, logging associated disturbance has still been sufficient to significantly alter resident bird community composition.

The majority of those birds found in significantly higher abundance in the unlogged areas of the La Chonta concession were associated with forest habitats dominated by large trees, or a high diversity of trees, providing dense canopy cover and deep leaf litter, with an understorey dominated by ferns (Figure 3, 4). These conditions are not indicative of the habitats created by logging activities. In La Chonta, skid trails, roads and landings disturb 25% of ground area with an additional 25% of the canopy opened due to tree felling (Jackson et al., 2002). Furthermore, logging gaps differ significantly from natural tree-fall gaps in size and the density and composition of understorey vegetation (Felton et al., 2006b). The introduction of logging roads and skidder trails, as well as the increased frequency and extent of tree-fall gaps, all contribute to a reduction in canopy continuity and the increased prevalence of forest area in early successional stages.

How a bird species responds to forest disturbance can be dictated, at least in part, by their direct physiological sensitivity to associated changes in microclimate (Thiollay 1992). Birds that forage exclusively in the lower understorey can be physiologically and behaviorally specialized for lower-light conditions (Stratford & Robinson, 2005). Neotropical species that evolved in the relatively stable forest understorey may be particularly intolerant to changes in microclimate (Canaday 1996; Stratford & Robinson 2005). Increased canopy-discontinuity that fragments these low light habitats may thereby reduce the availability of suitable foraging conditions for light-sensitive species.

For example, several insectivores, including the black-faced antthrush (*Formicarius analis*), were significantly less abundant in the harvested blocks of this study. Their apparent decline may be the result of three interrelated aspects of anthropogenic disturbance. First, members of this feeding guild are predicted to be particularly intolerant of habitat above threshold levels of irradiance (Stratford & Robinson 2005; Gray et al., 2007). Logging may therefore reduce the availability of adequate microclimatic foraging conditions with resultant impacts on insectivore population abundance (Barlow et al., 2006). Second, increased irradiance may also result in the loss of food resources, with xeric conditions in the understorey reducing the composition and abundance of arthropod food resources (Karr & Brawn 1990; Rosenberg 1990; Mason 1996; Barlow et al., 2002). Third, the presence of logging roads may have served to reinforce these declines.

In a study by Sekercioglu et al. (2002), the authors suggest that *Formicarius analis* is unable to recolonize suitable habitat within fragmented landscapes because their sensitivity to altered microclimates prevents them from crossing deforested areas. Previous research has established that roads as narrow as 10m can act as barriers to dispersal for understorey insectivores in the Neotropics (Develey & Stouffer 2001). Logging roads in La Chonta average 11.3m in width (Jackson et al., 2002) and are therefore potentially acting as linear barriers, severely restricting the ability of *F. analis* and other sensitive understorey species (eg. the spot-backed antbird *Hylophylax naevia*) to re-colonize suitable habitats.

Another bird species encountered significantly more often in the unlogged areas of the concession was the barred forest-falcon *M. rufficolis*. Our results suggest that this forest raptor may be adversely affected by reduced-impact logging because of its strong association with closed canopy forests. Forest falcons, such as *M. rufficolis*, are morphologically adapted to living and hunting in forest environments, possessing short wings and long tails that aid maneuverability in dense vegetation (Jullien & Thiollay 1996). As such, their non-detection within harvested blocks may be due to an overall decline in the suitability of appropriate vegetation structure, as has been the suggested reason for forest raptor declines from other logged sites (Jullien & Thiollay 1996).

Their absence from logged forest also may be associated with a lack of suitable nesting trees. One study conducted in Guatemala found that the majority of *M. ruficollis* nesting hollows were located in the cavities of trees belonging to the genus *Cedrela*, and were over the minimum diameter cut size used at La Chonta (Thorstrom et al., 1990). As both *Cedrela fisilis* and *Cedrela odorata* are harvested in the La Chonta concession (Park et al., 2005), it is possible that logging operations are reducing nesting options in harvested blocks. Notably three other species of falcon (collared forest-falcon (*Micrastur semitorquatus*), lined forest-falcon (*Micrastur gilvicollis*), and bat falcon (*Falco rufigularis*)) were also undetected within the harvest blocks.

Two large-bodied canopy feeding frugivores also appeared to be disproportionately sensitive to the reduced-impact logging conducted within this forest. Both the channel-billed toucan *Ramphastos vitellinus* and the white-throated toucan *Ramphastos tucanus*, were significantly less common in the harvested blocks of the concession. *R. vitellinus* and *R. tucanus* are both primarily frugivorous canopy feeders (Remsen et al., 1993; Galetti et al., 2000). They are of special interest to forest managers because toucans are considered to be very effective seed dispersers (Snow 1981). The beak of the toucan is large and dexterous and enables the toucan to consume fruit of varying sizes, from many different tree species (Galetti et al., 2000). Furthermore, their movement across large territories (estimated to be ca. 40-50ha in the Peruvian Amazon (Terborgh et al., 1990)) increase the dispersal and associated survival rates of seeds for timber tree species such as *Virola surinamensis* (Howe et al., 1985). In the case of this timber species, toucans were far more effective than smaller frugivorous birds at dispersing seeds to areas where they experienced lower mortality rates (Howe et al., 1985).

The primarily frugiviorous diet of *R. vitellinus* and *R. tucanus* raises the possibility that their reduced abundance results from a reduced availability of fruit. Many of the timber tree species harvested in La Chonta are important fruit sources for frugivorous birds (Mostacedo & Fredericksen 1999; Park et al., 2005). This is especially the case for the large free-standing fig *Ficus boliviana*. Fig trees are regularly considered keystone plant resources (eg. Leighton & Leighton 1983;

Terborgh 1986b) because their asynchronous fruiting habits, large size and copious fruit production (Janzen 1979) enable them to provide fruit during periods when other fruit resources are inadequate (Terborgh 1986b). Harvesting the largest individuals of *Ficus boliviana* and other timber species that produce fruit consumed by birds (eg. *Pseudolmedia laevis*), may therefore be reducing the availability of fruit during these periods of scarcity.

5.6.1 Conservation and management implications

There is currently active promotion of claims that RIL procedures applied within FSC certified concessions “conserve forest biodiversity” (FSC 2002) and can be considered to be “sustainable forest management” (WWF 2007). In comparison to the impacts of conventional selective logging practices often encountered in the tropics, these statements may be considered reasonable. However, to suggest with any confidence that a particular forestry management technique conserves forest biodiversity and/ or is ecologically sustainable would need to be supported by decades of research necessarily encompassing several harvesting cycles (Hartshorn 1995). As such, general claims regarding the capacity of certified RIL concessions to maintain biodiversity are currently unsubstantiated, with potentially serious repercussions if incorrect. First, unrealistic expectations regarding the biodiversity value of forests logged using RIL techniques could result in RIL entering fragile and biodiverse ecosystems where logging should be excluded. Second, these claims could provide a misleading perspective regarding the contribution that RIL is making to counteract the loss of biodiversity from large areas of disturbed tropical forest. For instance, in this study several species of conservation concern were either not encountered, or encountered in significantly lower abundances within the logged areas of the concession.

Keller et al (2007) argues that we must accept that forests selectively logged for commercial quantities of timber will “be different” from those that are not managed for commercial use. We agree with this assessment. However, we also suggest that what is acceptably “different” from a relatively pristine state must be clearly defined, and can not differ to the point of being unsustainable, especially for certified concessions. Unfortunately, the results of several studies suggest that current management practices employed within the La Chonta certified concession are not sustainable.

The dominance of non-commercial pioneer plant species in logging gaps (Park et al., 2005), lack of adequate regeneration for most commercial species (Pariona et al., 2003), and current projections of dramatic declines in the volume of future harvests (Dauber et al., 2005), are strong indications that currently employed logging practices in this concession are unsustainable. If the forest continues to be harvested at a rate that exceeds its capacity to regenerate, then eventually reductions in timber yield will lower the economic incentives for maintaining the concession. Under these circumstances there is a significant risk that the concession could be converted to potentially more profitable land-uses, such as agriculture or pastural lands. This would result in the degradation and clearing of a far higher percentage of the original forest than found in even the most exploitative of selective logging operations. Inevitably such a landscape transformation would equate with a substantial loss of forest dependent biota, including many of the bird species currently found within the La Chonta concession. It is our view that the types of changes to forestry practice which may redress this imbalance between harvesting rates and forest regeneration will potentially also benefit some of the bird species that appear to be adversely affected by current logging activities. This is because the same altered microclimatic conditions that disadvantage the regeneration of some commercial tree species (see Felton et al., 2006b), also appear to be unfavourable to some forest-dependent avian taxa.

For example, nearly one quarter of all skid trails in the La Chonta concession are dead-ends or short cuts and are not used for the transportation of logs (Jackson et al., 2002). These unnecessary trails are causing 79% of all ground area disturbance outside of the marked trail network (Jackson et al., 2002). Correcting this problem would substantially reduce the extent of damage to forest understorey, and limit the amount of disruption to canopy continuity. These changes would also help to reduce incidental damage to commercial tree species in advanced stages of regeneration (see Felton et al., 2006b), and potentially redress one of the causal processes behind avian species declines.

Consideration should also be given to the true long term costs and benefits of harvesting the free-standing fig species *Ficus boliviana*. This tree species regularly achieves a dbh of >200cm and possesses a crown often exceeding 30m in diameter

(Felton pers. obs.). The harvesting of this tree is disproportionately contributing to canopy discontinuity (Felton et al., 2006), and potentially removing a valuable keystone fruit resource for the frugivorous species of this forest. As the seed dispersing activities of both *R. vitellinus* and *R. tucanus* are presumably contributing to forest regeneration, there is the possibility that reducing the numbers of these large avian frugivores could have negative flow-on effects for the ecology of this forest.

It is currently unknown whether the processes that are causal to the observed differences in bird community composition will have time to recover between timber harvests, or be exacerbated by subsequent harvests. If the processes that are leading to the apparent declines of some bird species within the harvested areas of the concession are operating at a temporal scale that allows for recovery within the projected logging rotation cycle, then it is possible that at least some bird species may be able to maintain viable populations by moving from areas currently being harvested to regenerating or pristine areas of the concession (Wunderle et al., 2006). However, if some bird species are declining as a result of causal processes that will not be rectified, or in fact will be exacerbated with each consecutive harvest, then further changes to bird communities can be expected unless logging practices are altered and/or rotation times extended. Further research assessing longer-term changes to the bird community needs to be conducted so that we can determine to what extent these scenarios are occurring in La Chonta. Subsequently, species orientated research could be used to identify the causal processes behind declines (Lindenmayer et al., 2007) so that contributing factors to these declines can be minimized through negotiations with concession managers.

5.6.2 Conclusion

There is increasing evidence that reduced-impact logging of tropical forests causes less damage to forest structure in the tropics than conventional selective logging techniques (Asner et al., 2004a; Huth et al., 2004). Furthermore, prohibitions on hunting are laudable improvements that contribute to the conservation of birds and mammals of this and other certified forestry concessions (Wilkie et al., 1992; Peres 1997, 2000). However, achieving such improvements relative to the exploitive nature of conventional selective logging can come with the risk of complacency. There is as yet insufficient data to suggest that RIL is a panacea for combining the commercial need for forest products with the need to maintain those ecosystems that provide them. Our findings suggest that at least some bird species, representing a range of ecological guilds, are at risk of decline in tropical forestry concessions that employ RIL techniques. With more knowledge, and strong links between science and policy, it is possible that any necessary adjustments can be made, and RIL can be seen as the first step towards the difficult and complex goal of achieving ecologically sustainable forestry in the tropics.

5.7. Acknowledgements

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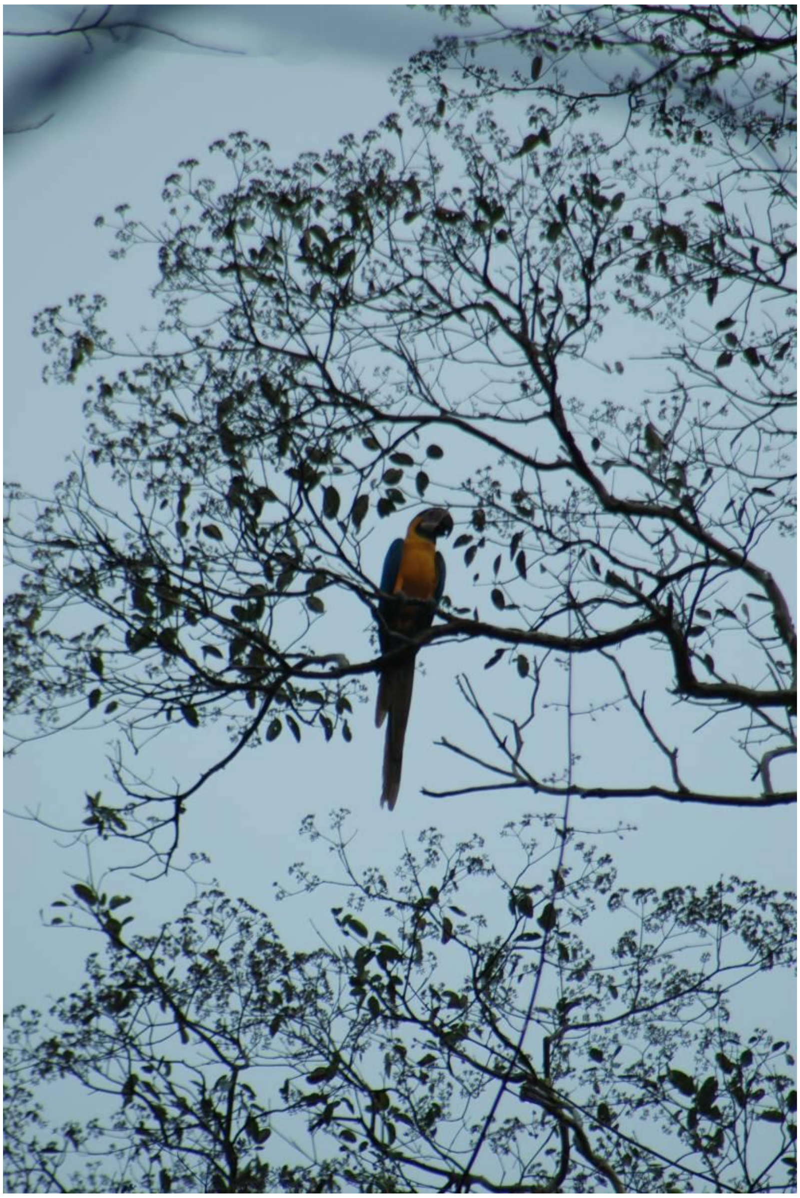

*Blue and yellow macaw (*Ara ararauna*)* Photo by Helga Peters

Chapter 6

A COMPARISON OF BIRD COMMUNITIES IN THE ANTHROPOGENIC AND NATURAL TREE-FALL GAPS OF A REDUCED-IMPACT LOGGED BOLIVIAN SUBTROPICAL FOREST

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6.1. Abstract

We studied bird community composition and abundance within four vegetation and disturbance categories located within selectively logged and unlogged forest in a Bolivian subtropical lowland forestry concession. The logged forest was subject to reduced-impact logging between 1 and 4 years prior to our study. The four categories were: 1) ‘gap’ points possessing natural or anthropogenic tree-fall gaps; 2) ‘target’ points with one of five commercial tree species of harvestable size; 3) ‘future’ points possessing a commercial tree below harvestable size; and 4) ‘non-target’ points not possessing harvestable tree species. The bird community composition of logging gaps significantly differed from that found within natural tree-fall gaps in the unlogged forest (p<0.05). Species richness was higher in natural tree-fall gaps than in anthropogenic gaps. Furthermore, a higher proportion of disturbance sensitive species were associated with natural-tree fall gaps, whereas a higher proportion of disturbance tolerant species were associated with anthropogenic gaps. No significant

difference was detected in the bird community composition for the other three vegetation categories surveyed. We discuss the conservation and silvicultural repercussions of these results.

6.2. Introduction

Tropical forests are the most species-rich of all terrestrial ecosystems (Turner 1996), and their preservation will be an integral component of successful global conservation efforts (Groombridge & Jenkins 2002). Of the anthropogenic processes threatening tropical forests, there is increasing evidence that selective logging can rival deforestation in the total amount of tropical forested area being degraded (Asner et al., 2005). Selective logging is the dominant form of timber extraction in the tropics (Rametsteiner & Simula 2003), and involves the periodic extraction of large, and well-formed representatives of a forest’s commercially valuable tree species (Johns 1988b). The extent to which “selective logging” degrades forest structure varies considerably, depending on extraction rates and the extent of collateral damage to the residual stand (Johns 1988b). As a term, “selective logging” therefore represents a continuum of anthropogenic disturbance, ranging from deforestation at one extreme to extensive canopy and vegetation structure retention at the other (van Soest 1998). It is expected that somewhere along this continuum, prescriptions for selective logging can be developed that successfully combine economically viable levels of timber extraction with biodiversity conservation (Pinard & Putz 1996a). Reduced-impact logging (RIL) is being developed in response to this need.

RIL is a form of selective logging increasingly employed in tropical forests. It incorporates a variety of techniques aimed at lowering levels of damage to the residual stand (Putz et al., 2001). These include directional felling, pre-harvest vine cutting, and preliminary inventories to reduce the number and density of logging roads (Heinrich 1995). Recent studies suggest that reduced-impact logging of tropical forests causes less damage to forest structure than conventional selective logging techniques (Asner et al., 2004a; Huth et al., 2004). However, reduced-impact logging is still a form of commercial forestry that can disturb vegetation structure (Jackson et al., 2002), and thus impact on some forest dependent species (Bojanic & Bulte 2002; Dauber et al., 2005), such as birds.

Bird community composition is strongly determined by vegetation structure (MacArthur et al., 1966; Gilmore 1985; Wiens 1992). The structural characteristics of forest plant communities support some of the vital requirements of 'habitat' for birds, including those for reproduction, shelter, predator avoidance and foraging efficiency (Holling 1992). Disturbance to vegetation-structure does not however necessarily equate with loss of habitat for forest dependent bird species (Lindenmayer & Fischer 2006). This is because disturbance is an integral part of forest ecosystems (Schemske & Brokaw 1981; Attiwill 1994), and under natural conditions can vary spatially and temporally from frequent low intensity disturbances at the scale of individual tree-falls, to infrequent landscape scale high intensity events (eg. fires, severe storms) that can significantly alter entire stands (Coates & Burton 1997). Each bird species will react differently to forest disturbance depending (in part) on its habitat specialization, foraging behaviour, diet adaptability and physiological sensitivity to microclimatic changes (Thiollay 1992; Barlow & Peres 2004; Wunderle et al., 2005; Wunderle et al., 2006; Gray et al., 2007). For instance, tree falls, and the gaps they create, represent a source of numerous relatively small scale disturbances within a forest that are simultaneously a source of habitat for some birds, and a loss of habitat for others. For this reason, studies of bird species' responses to tropical forest disturbance have reported negative, positive or neutral impacts on population size and/or demographics, depending on the extent of disturbance and the associated impact on the availability of habitat for the species being considered (Hill & Hamer 2004).

The most species-rich avian communities in the world are found in Neotropical forests (Ridgely & Tudor 1994; Turner 1996). Research findings from conventional selective logging (Mason 1996), and other forms of forest disturbance within the Neotropics (Aleixo 1999) suggests that it will be those bird species closely associated with specific vegetation types targeted by logging which will be most likely to decline in population size, or express negative demographic responses to RIL (Thiollay 1997). For example, species that typically decline from forests subjected to conventional selective logging are often restricted to specific vegetation types, such as the understorey in tall forests (Canaday 1996; Thiollay 1997). In contrast, those species which are favoured by anthropogenic disturbance are generally ubiquitous even in secondary forests (Thiollay 1997; Aleixo 1999).

Previous research on vegetation structure within a reduced-impact logged forest in the subtropical lowland province of Santa Cruz, Bolivia, demonstrated that logging gaps created by reduced-impact logging were not the anthropogenic equivalents of natural tree-fall gaps (Felton et al., 2006a). In this paper we assess whether the bird communities of a reduced-impact logging concession differ; i) within anthropogenic and natural tree-fall gaps, and ii) within comparable vegetation categories of the harvested and unharvested areas of the concession. We discuss our results in relation to current expectations regarding the compatibility of RIL associated disturbance with biodiversity maintenance.

6.3. Methods

6.3.1. Site description

Our study area was located in the lowland subtropical humid forest of the Guarayos Forest Reserve, Department of Santa Cruz, Bolivia. Research was conducted in the 100 000 ha forestry concession “La Chonta”. This is owned and managed by Agroindustria Forestal La Chonta (509000 to 545000 easting, 8275500 to 824900 northing; Figure A2.1.). The forest has an average elevation of 320 m (range 230-390m). The soils consist of oxisols, ultisols, and inceptisols (Park et al., 2005). The mean annual temperature is 25°C with a mean annual precipitation of approximately 1 560 mm. The region experiences a distinct dry season from May to October. The entire concession was subjected to legal and illegal selective logging of mahogany (*Swietenia macrophylla*), and Spanish cedar (*Cedrela odorata*) 10 – 25 years prior to this study. The concession was certified by SmartWood in 1998.

6.3.2. Harvesting procedure

Approximately 2 500 ha was harvested each year over three contiguous 850 ha blocks (~4 km x 2 km), yielding 50 000 m^3 of timber annually. Eighteen commercial tree species were harvested during the time of this study (2003-2004) including *Ficus boliviana*, *Hura crepitans*, *Terminalia oblonga*, *Pseudolmedia laevis*, *Cariana ianeirensis*, and *C. estrellensis*. Average harvest intensity was approximately 4 trees/ha (Jackson et al., 2002). The forestry company Agroindustria Forestal La

Chonta conducts inventories of harvestable trees one year prior to logging. The minimum size for harvest is 50 cm diameter at breast-height (dbh) for all species except *F. boliviensis* and *H. crepitans*, which are harvested above 70 cm dbh. One in five harvestable trees is required by law to be left as a seed tree. During pre-harvesting inventory, trees selected for felling are cleared of all vines on the bole.

The forestry company uses a 'fishbone' harvesting strategy with a single primary north-south road bisecting each 850 ha block. Skid trails are located 100-150 m apart and run in an east-west direction on either side of the primary road. Chainsaw teams trained in directional felling techniques try to reduce damage to the residual stand during felling. Removal and loading of boles is conducted using rubber-tired skidders to reduce soil compaction. It is intended that blocks be re-cut in 25 to 30 years, and unlogged areas of the concession were destined to be logged from 2004-2007.

6.3.3. Survey design

Because selective logging disproportionately disturbs forest with commercial densities of harvestable trees, a stratified-random sampling design was used which incorporated commercial tree species occurrence, vegetation height, and disturbance type. This design increased the likelihood that logged and unlogged survey points were appropriate for comparison, accounted for natural variation in vegetation structure, and enabled us to distinguish between different disturbance types. The four vegetation categories were: 1. 'target' points (T) with vegetation height over 20 m and possessing one of five commercial tree species of harvestable size (*Ficus boliviensis*, *Hura crepitans*, *Cariniana estrellensis*, *C. ianeirensis*, *Terminalia oblonga*); 2. 'future' points (F) from 12-20 m in height and possessing an individual of the afore mentioned five species not yet of harvestable size but above 30 cm dbh; 3. 'non-target' points (N) of less than 12m in height and not possessing commercial trees above 10 cm dbh; and 4. 'gap' points (G) possessing a tree-fall gap caused by the felling of a tree (in the harvested blocks) or a natural gap created by a tree (in the unlogged blocks) of greater than 50 cm dbh. In the logged forest, the 'target' category was represented by seed trees left by loggers to aid regeneration. Trees not harvested due to undesirability (eg. insufficient bole length or malformation) were not included in this category. In total, 96 points was surveyed, represented by 24 points of each of the four vegetation categories equally divided between the logged and unlogged areas of the concession.

We conducted vegetation structure and floristic surveys at all survey points during June and July 2004. At each point, a 20 m x 20 m quadrat was marked within which we quantified aspects of canopy cover, canopy height, understorey density, tree species diversity, basal area, and other aspects of vegetation physiognomy and floristics. For details of vegetation sampling design see Felton et al. (2006).

6.3.4. Bird surveys

At each of the 96 survey points, we used the point-count method of surveying bird species abundance. Only birds observed less than 20m from the observer were included in analyses, due to the need to couple bird species occurrences with vegetation categories. This relatively small radius was also used to minimize the potential for biases affecting the detectability of birds when surveying in habitats that vary substantially in vegetation structure (Verner 1981; Verner & Ritter 1988; Waide & Narins 1988; Petit et al., 1999). To reduce the effects of seasonal variation on bird abundance/presence, logged and unlogged areas were surveyed on alternate days. All survey points were located at least 300 m from the nearest other point, and at least 500 m from the edge of neighbouring treatment blocks. Surveys were conducted from December to February of the 2003-2004 wet season. One observer (A.F.) completed all surveys. Surveys began at first light (5:45-6:00 am), and continued until approximately 7:30 am. This period overlapped with 1. the daily peak in bird vocal activity (pers. obs. A.F.), and more specifically 2. with the time period when those bird families that are sensitive to logging disturbance in the La Chonta concession are most active, and therefore most likely to be detected during surveys (Woltmann 2005). Each dawn survey consisted of visiting one point of each of the four habitat types. Each point was surveyed for 12 minutes. We included birds flushed from the survey point on approach by the observer, while birds flying over the survey area were not included in the analysis.

Due to the density of forest vegetation, most identifications were made acoustically, rather than visually. In addition to point counts, recordings of birds also were made using a Sony TCM 5000 tape-recorder that was attached to a Sennheiser ME66 microphone. These recordings were used as a supplement to in-the-field identification of vocalizing species. For unidentified species, symbolic representations of songs were noted. This was in addition to notes on the recording time, direction, and estimated distance to the call. This enabled the matching of subsequent identifications with abundance and distance information. Unknown recordings were identified using the CD-ROM Birds of Bolivia, 2.0 (Mayer 2000), or by an expert (B.H). Survey results were used as a crude surrogate of relative abundance, rather than as estimates of absolute density.

6.3.5. Statistical analysis

Bird species recorded only once during surveys were removed from analysis. We used correspondence analysis (Greenacre 1984) to reduce the dimensionality of each data set. Scores were obtained for the first three axes, which accounted for the majority of variation in the data. General linear regression (Timm & Mieczkowski 1997) was applied sequentially using each of these two axes to determine whether a given habitat category (eg. “non-target”) differed significantly in terms of bird community composition and abundance between the logged and unlogged habitats. Jaccard’s index of similarity (Krebs 1998) was calculated to facilitate comparison with previous studies of logging impacts on tropical bird communities.

The Indicator Value (IV) procedure (Dufrêne & Legendre 1997) was used to test associations between individual bird species and anthropogenic or natural tree-fall gaps. IndVal is a percentage that ranges from 0 to 100 with the maximum value afforded when a species is present only in one habitat type and occupies all sites within that habitat. Higher IV values therefore indicate species which are more representative for the given habitat. A random reallocation procedure using 1000 iterations was conducted to test the significant level of IndVal results (alpha=0.05).

6.4. Results

During dawn point-count surveys, we identified approximately 1 150 birds, belonging to 123 species, representing 32 families. Of the four habitat categories, bird community composition and abundance significantly differed between logged and unlogged gaps (Table 6.1.). “Non-target”, “future target”, and “target” habitat categories were similar in terms of bird community composition and abundance between the logged and unlogged areas (Table 6.1). Logged and unlogged gaps had the lowest overlap in species composition of the four habitat categories as determined by the Jaccard index of similarity (Table 1). Species richness was higher in natural-tree fall gaps (Table 6.1). Structural characteristics of natural and anthropogenic tree fall gaps found in the logged and unlogged forests are presented in Table 6.2.

Results of the Indicator Value (IV) method are presented in Table 3 and 4. The twenty species with the highest IV score are listed in descending order of association with unlogged gaps (Table 6.3) and logged gaps (Table 6.4). Random reallocation permutations demonstrated that *Formicarius analis* is significantly more associated with natural tree-fall gaps than with anthropogenic gaps. IndVal scores are used to indicate the relative contribution of bird species to the established differences in bird community composition between anthropogenic and natural tree-fall gaps. Six of the 20 species with the highest IV association with the unlogged gaps, were found to be significantly less abundant overall in the logged versus the unlogged areas of the La Chonta concession (Table 6.3). Three bird species exhibiting the opposite trend (ie. with a significantly higher prevalence in the logged versus unlogged gaps), were amongst the 20 species with the highest IV association with the logged gaps (Table 6.4). Birds that were considered to exhibit a ‘high’ sensitivity to disturbance (Stotz et al., 1996), were more prevalent in natural-tree fall gaps (50% of species) than in anthropogenic gaps (20% of species). Birds that were considered to exhibit a ‘low’ sensitivity to disturbance (Stotz et al., 1996), were four times more prevalent in anthropogenic gaps (20% of species) than in natural-tree fall gaps (5% of species) (see Table 6.3 & 6.4).

Table 6.1. General linear regression of the primary axis of correspondence analysis for bird community composition and abundance within habitat categories located in the logged and unlogged forests of the La Chonta concession, Department of Santa Cruz, Bolivia. Species richness and results from the Jaccard similarity index are also provided.

Habitat category	*Number of species*		*Jaccard similarity*	*Statistical result*
Unlogged vs. Logged	*Unlogged*	*Logged*	*index*	*P value*
Gap	56	49	0.42	<0.05
Non-target	51	43	0.45	n.s.
Future target	50	48	0.48	n.s.
Target	56	48	0.46	n.s.

Table 6.2. Selected structural measurements (mean +/- SE) distinguishing amongst 22 variables relating to vegetation structure within natural and anthropogenic gaps in the reduced impact logged area of the subtropical humid forests of the la Chonta forestry concession, Santa Cruz, Bolvivia. S.E. stands for standard error. Modified from Felton et al. (2006a)

Structural measurements	Unlogged Mean +/- SE	**Logged** Mean +/- SE
# of tree species / 0.04ha	8.4 +/- 0.5	7.7 +/- 0.5
# of trees / 0.04ha	14 +/- 1	11.5 +/- 0.7
Canopy height (m)	9.8 +/- 0.8	11 +/- 0.8
Canopy cover (%)	91 +/- 1.1	88 +/- 1.5
# of poles / 0.04 ha	24.1 +/- 1.5	24.5 +/- 1.9
Leaf litter depth	2.1 +/- 0.1	1.9 +/- 0.1
Fern % cover	28.3 +/- 2.7	23.9 +/- 2.3
Basal area sq. m. / 0.04ha	0.5 +/- 0.1	0.5 +/- 0.1
Leaf litter % cover	80 +/- 1.6	79 +/- 1.8
Erythrochiton fallax % cover	5 +/- 2.3	1 +/- 0.7
Palm % cover	1.4 +/- 0.5	2.2 +/- 0.6
# Flower plants / 0.04ha	15.2 +/- 3	11.5 +/- 3
# fruiting plant / 0.04ha	1 +/- 0.3	0.4 +/- 0.1
Seedling % cover	13.3 +/- 1.7	23.6 +/- 2.2
Understorey density (0-20)	5.3 +/- 0.5	6.8 +/- 0.5
# of palms / 0.04ha	0.7 +/- 0.5	1.1 +/- 0.8
Vine high % cover	10.7 +/- 2.1	3.8 +/- 1
Bare ground % cover	4.3 +/- 0.8	3.3 +/- 0.8
Vine low % cover	19.9 +/- 2.7	13.7 +/- 1.9
Heliconia spp. % cover	15 +/- 2.5	20 +/- 3.2
Gap size (m^2)	404.5 +/- 52.4	638.2 +/- 76.9

Table 6.3. The twenty bird species with the highest Indicator Value (IV) for unlogged gaps, representing the degree to which a given species is associated with unlogged (U) versus logged (L) gaps in the La Chonta concession, Department of Santa Cruz, Bolivia. The number of observations for a given species in logged or unlogged gaps is also presented. "Sensitivity" to disturbance ratings are low (L), medium (M) and high (H), as per Stotz et al. (1996). Species marked with an asterisk are significantly less common in the harvested areas of the concession (A. Felton unpublished data)

Family	Common name	Scientific name	Logged	Unlogged	IV	Sensitivity	Foraging guild
Thamnophilidae	rufous-winged antwren	Herpsilochmus rufimarginatus	11	12	39.13	M	Gleaning insectivore
Dendrocolaptinae	buff-throated woodcreeper	Xiphorhynchus guttatus	7	8	35.56	M	Bark-dwelling insectivore
Formicariidae	black-faced antthrush	Formicarius analis*	0	5	33.33	M	Terrestrial insectivore
Trogonidae	collared trogon	Trogon collaris*	0	5	25.00	M	Insectivre
Cotingidae	Screaming Piha	Lipaugus vociferans	3	6	22.22	H	Frugivore
Columbia	gray-fronted dove	Leptotilla rufaxilla*	0	2	16.67	M	Frugivore
Ramphastidae	channel-billed toucan	Rhamphastos vitellinus*	0	4	16.67	H	Frugivore/omnivore
Thamnophilidae	white-flanked antwren	Myrmotherula axillaris	0	2	16.67	M	Gleaning insectivore
Trochilidae	white-bearded hermit	Phaethornis hispidus	0	2	16.67	M	Nectarivore
Tyrannidae	Snethlage's tody-tyrant	Hemmitricus minor	0	2	16.67	H	Gleaning insectivore
Tyrannidae	flammulated bamboo-tyrant	Hemmitricus flammulatus	0	2	16.67	M	Gleaning insectivore
Tyrannidae	dusky-capped flycatcher	Myiarchus tuberculifer	2	4	16.67	L	Sallying insectivore
Columbia	ruddy pigeon	Columba subvinacea	0	1	8.33	H	Frugivore
Dendrocolaptinae	barred woodcreeper	Dendrocolaptes certhia	0	1	8.33	H	Bark-dwelling insectivore
Falconidae	barred forest-falcon	Micrastur ruficollis*	0	1	8.33	M	Raptor
Picidae	red-necked woodpecker	Campephilus rubricollis*	0	2	8.33	H	Bark insectivore
Bucconidae	white-fronted nunbird	Monasa morphoeus	0	1	8.33	H	Sallying insectivore
Columbia	plumbeous pigeon	Columba plumbea	0	1	8.33	H	Frugivore
Dendrocolaptinae	lineated woodcreeper	Lepidocolaptes albolineatus	0	1	8.33	H	Bark-dwelling insectivore
Ramphastidae	chestnut-eared aracari	Pteroglossus castanotis	0	1	8.33	H	Frugivore

Table 6.4. The twenty bird species with the highest Indicator Value (IV) for logged gaps, representing the degree to which a given species is associated with logged (U) versus unlogged (L) gaps in the La Chonta concession, Department of Santa Cruz, Bolivia. The number of observations for a given species in logged or unlogged gaps is also presented. "Sensitivity" to disturbance ratings are low (L), medium (M) and high (H), as per Stotz et al. (1996). Species marked with an asterisk are significantly less common in the harvested areas of the concession (A. Felton unpublished data)

Family	Common name	Scientific name	Logged	Unlogged	IV	Sensitivity	Foraging guild
Tyrannidae	forest elaenia	Myiopagis garmardii	9	5	42.86	M	Sallying insectivore
Thamnophilidae	plain antvireo	Dysithamnus mentalis	8	3	42.42	M	Gleaning insectivore
Thraupinae	red-crowned ant-tanager	Habia rubica	7	4	37.12	H	Insectivore/omnivore
Cardinalinae	blue-black grosbeak	Cyanocompsa cyanoides	4	1	26.67	M	Omnivore
Dendrocolaptinae	cinnamon-throated woodcreeper	Dendrexetastes rufigula	4	0	25.00	H	Gleaning insectivore
Motmotidae	blue-crowned motmot	Motmotus motmota	3	0	25.00	M	Sallying insectivore
Thamnophilidae	black-throated antbird	Myrmeciza atrothorax*	3	0	25.00	L	Gleaning insectivore
Tinamidae	little tinamou	Crypturellus soui*	5	2	23.81	L	Terrestrial granivore
Tinamidae	undulated Tinamou	Crypturellus undulatus	4	1	20.00	L	Terrestrial granivore
Parulinae	golden-crowned warbler	Basileuterus culicivorus*	3	1	18.75	M	Insectivore/omnivore
Furnariinae	buff-throated foliage-gleaner	Automolus ochrolaemus	3	0	16.67	M	Gleaning insectivore
Picidae	white-throated woodpecker	Piculus leucolaemus	2	0	16.67	M	Bark-dwelling insectivore
Thamnophilidae	spot-backed antbird	Hylophylax navia	2	0	16.67	H	Gleaning insectivore
Trochilidae	reddish hermit	Phaethronis ruber	4	2	16.67	M	Nectarivore
Tyrannidae	yellow-margined flycatcher	Tolmomyias assimilis	2	0	16.67	H	Sallying insectivore
Emberizinae	pectoral sparrow	Arremon taciturnus	3	1	12.50	M	Omnivore
Pipridae	firey-capped manakin	Machaeropterus pyrocephalus	3	1	12.50	M	Frugivore
Dendrocolaptinae	olivaceous woodcreeper	Sittasomus griseicapillus	2	1	11.11	M	Bark-dwelling insectivore
Trogonidae	black-tailed trogon	Trogon melanurus	2	1	11.11	M	Omnivore
Bucconidae	gray-cheeked nunlet	Nonnula ruficapilla	1	0	8.33	L	Sallying insectivore

6.5. Discussion

Natural tree-fall gaps supported higher bird species richness than anthropogenic tree-fall gaps. Bird community composition was also significantly different between natural tree-fall gaps and logging gaps in this RIL concession. Furthermore, fifty percent of those bird species which were more associated with natural tree-fall gaps are considered to be (Stotz et al., 1996) relatively "vulnerable to human disturbance". This indicates that natural-tree fall gaps support species of higher conservation importance than anthropogenic gaps. We consider that two, potentially synergistic, causal processes may be driving these differences. First, fundamental differences in the type of habitat created by natural and anthropogenic gaps may be supporting different avian assemblages. Second, differences in the bird community composition and abundance of the surrounding residual stand may be leading to corresponding changes in the bird assemblages found within anthropogenic gaps. The distinction between these processes is primarily one of scale. Presence and abundance of individual bird species within a gap will be driven by such things as habitat selection, foraging behaviour, mating systems, and population dynamics. These responses will be influenced both by conditions experienced at the scale of the gap, and at the larger spatial scale of the surrounding forest (Mitchell et al., 2006). We discuss these two causal processes below.

6.5.1. Within gap processes

Gaps created by reduced-impact logging practices are quantifiably different from gaps caused by natural processes. Logging gaps were larger in size, differed in terms of microclimatic variables, were significantly lower in understorey density, and differed in the composition of regenerating vegetation (See Table 2. Jackson et al., 2002; Felton et al., 2006a). Differences in bird community composition and abundance within logging gaps may therefore be the direct result of either microclimatic differences, and/or the associated changes in vegetation structure and phylogeny (Hasui et al., On-line early).

Neotropical species that evolved in the relatively stable understories of closed-canopy forest can be directly intolerant of the altered microclimates within larger gaps (Canaday 1996; Stratford & Robinson 2005). This may be due to physiological and behavioral sensitivity to increased-light conditions (Stratford & Robinson 2005). For example, the black-faced anthrush (*Formicarius analis*), a ground antbird belonging to the family Formicariidae, occurred in over 40% of unlogged gaps, but was never detected in the logging gaps. Members of this family are known to be intolerant of disturbance (Barlow et al., 2002; Ferraz et al., 2003), particularly within habitats experiencing levels of irradiance above a threshold level (Sekercioglu et al., 2002). The large canopy openings created by logging gaps in the La Chonta concession means that these areas are more likely to have passed a microclimatic toleration-threshold for bird species such as *F. analis*.

These microclimatic conditions, and the associated flush of dense vegetation, potentially result in the altered availability, or accessibility, of different types of invertebrate prey (Didham et al., 1996). As insectivores use a variety of different foraging methods and capture prey at varying heights and on different substrates, it is not surprising to find differences in the relative composition of insectivorous species (belonging to different foraging guilds), within logging gaps and gaps created by natural tree falls (see Tables 3 and 4). These differences may be further accentuated by pre-harvest liana cutting. As lianas provide a distinct foraging substrate, those birds which are obligate or facultative liana foragers, may be detrimentally effected by this practice (Barlow et al., 2006). As the practice of pre-harvest liana cutting is successfully reducing liana loads in logging gaps (Felton et al., 2006a), it is possible that this practice influences the availability of suitable habitats within natural and anthropogenic gaps.

Research by Hasui *et al.* (On-line early) suggests that the abundance of obligate frugivorous bird species is strongly influenced by the availability of key plant species providing the necessary fruit production. Conversely, bird species with more insectivorous/ generalist diets, may be primarily influenced by variation in habitat structure, which can alter both the availability of prey items, and the bird species' foraging efficiency (Hasui et al., On-line early). There was a distinct difference in the number of bird species belonging to each of these guilds in the anthropogenic and natural tree fall gaps.

Natural-tree fall gaps supported higher numbers of frugivorous species, whereas anthropogenic tree-fall gaps supported higher numbers of insectivore/omnivores and omnivores. The increased numbers of insectivore/omnivores and omnivores within anthropogenic tree-fall gaps may be arising due to associated changes in vegetation structure resulting in increased availability of perches, prey, or a general improvement in prey visibility (Cody 1980). For frugivorous birds, the harvesting of fruit bearing timber tree species such as *Ficus boliviana*, and *Pseudolmedia laevis* (Woltmann 2003), may be contributing to their decreased abundance in anthropogenic tree-fall gaps. Although there was an expectation that increased light levels within logging gaps will result in a post-harvest fruiting bloom (Schemske & Brokaw 1981; Lambert 1992; Wunderle et al., 2006), either this did not occur, or it was insufficient to compensate for the removal of fruit bearing tree species (Table 2).

Logging gaps in La Chonta concession did however have a greater percentage of plants in flower than their natural counterparts in the unlogged forest (Felton et al., 2006a). Certain avian guilds (eg. nectarivores) may therefore increase in abundance following selective logging due to the increased availability of nectar in logging gaps, and other areas of canopy discontinuity (Mason 1996). Part of the altered bird species community composition and abundance in this study (eg. the reddish hermit *Phaethornis ruber*) may be a direct response to differences in the availability of nectar.

6.5.2. Influence of conditions in the surrounding forest

We did not detect significant differences in bird communities within the “target”, “non-target”, and “future” vegetation categories used in this study. However, as these vegetation categories were specifically placed within areas of the forest not directly altered by logging, the only potential logging associated disturbance in these treatments would be of an indirect nature. Comparison of understorey vegetation within these vegetation categories between the unlogged forest and the residual stand of the harvested forest, suggests that it takes four years or more before nearby canopy disturbance could alter regeneration patterns of understorey vegetation within adjacent undisturbed residual stand (A. Felton unpublished data). Prior to this elapsed time, any differences in understorey vegetation appear to be within the range of natural habitat heterogeneity, and therefore do not appear to be altering bird community composition at this scale of assessment.

Logging-related disturbance throughout the harvested areas of the concession may nevertheless influence the presence and abundance of at least some species within natural and anthropogenic gaps. Several species found at significantly higher overall abundance in the unharvested blocks (see Table 3), were found only within natural tree-fall gaps in the unlogged forest in this study. A similar trend was observed, for example, for the black-throated antbird (*Myrmeciza atrothorax*). This species was significantly more abundant in the harvested areas of the concession, and was only found within logging gaps of the harvested areas of the concession in this study. This indicates that conditions experienced at the scale of the residual stand or surrounding unlogged forest may contribute to differences in bird community composition within anthropogenic and natural tree-fall gaps.

For example, the channel-billed toucan (*Ramphastos. vitellinus*) is a primarily-frugivorous canopy feeder (Remsen et al., 1993; Galetti et al., 2000) that moves across territories of approximately 40-50ha in the Peruvian Amazon (Terborgh et al., 1990). Toucan movements are thought to be largely dictated by their need to follow the availability of fruit (Graham 2001). In the La Chonta concession, many of the harvested timber trees are also important fruit sources (Mostacedo & Fredericksen 1999; Park et al., 2005). The reduced abundance of *R. vitellinus* within the logging gaps of the harvested areas of the concession is therefore likely to result from concession-wide reductions in fruiting tree resources. This may explain the absence of the channel-billed toucan from logging gaps in the harvested areas of the concession, rather than processes operating at the scale of conditions experienced within a particular gap.

6.5.4. Conservation and management implications

Current silvicultural practices are creating gaps significantly larger than their naturally formed counterparts in the unlogged forests of the concession. These anthropogenic gaps are unlikely to provide conditions favourable to the physiological adaptations of some understorey avian species; or beneficial to the regeneration of some commercial tree species (see Felton *et al.* 2006). The end result was that anthropogenic tree-fall gaps provided habitat for fewer species in general, and more importantly, fewer species considered sensitive to human disturbance. Reducing the extent of canopy disturbance where possible, and limiting the commercial harvest of potential keystone fruit resources (eg. *Ficus boliviana*), may concomitantly address concerns regarding the long-term sustainability of timber production (Pariona et al., 2003), and the biodiversity maintenance capacity of this concession.

We support calls for forest management to be as consistent as possible with natural disturbance processes (Lindenmayer & McCarthy 2002; Messier &

Kneeshaw 2003). However, we also reiterate the views expressed by Manning *et al.* (2004), who warned against the temptation to substitute what we perceive as habitat, with the “Umwelt”, or the world as perceived by the species being considered (Manning et al., 2004). Gaps created by logging activities do not necessarily represent habitat to species occurring in natural gaps (Thiollay 1992). Despite the superficial resemblance of RIL gaps, to gaps caused by natural tree falls (Whitman et al., 1998), changes in bird community composition and abundance within anthropogenic gaps in this study suggests that the two disturbance processes are not interchangeable. These differences are directly relevant to those considering the compatibility of tropical RIL concessions with biodiversity maintenance.

6.6. Acknowledgements

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Chapter 7

CONCLUSION

This thesis has contributed to the understanding of the changes to forest structure associated with reduced-impact logging techniques, and how these changes can alter forest ecology. It also refined our understanding of how such changes can affect avian diversity and the composition of assemblages. The aim of this concluding chapter is to provide a brief synthesis of the key findings from the earlier chapters. To avoid undue repetition this chapter is presented as a short synopsis.

Chapters 2 and 3 focused on changes to vegetation structure and disturbance processes resulting from RIL in the La Chonta concession. Chapter 2 suggested that current silvicultural practices are potentially negating the benefits of increased seedling density found within logging gaps, by creating gaps with the microclimatic conditions preferentially beneficial to the regeneration of non-commercial pioneer species. I propose that this problem can be further exacerbated through damage to shade-tolerant species in advanced stages of regeneration during tree felling and bole removal. Research is now needed to quantify the damage caused to commercial tree species in advanced stages of regeneration from each component of the felling and bole removal process. Chapter 3 emphasized the need to consider changes to the understorey vegetation structure and phenology of the residual stand. The trajectory of these forested areas will be an important determinant of the ecological and economic future of Bolivian concessions. The results of Chapters 2 and 3 demonstrated the need for reassessment of anthropogenic disturbance processes employed in these forests.

If differences between human disturbance and natural disturbance remain large for a prolonged period, and the forest continues to be harvested at a rate that exceeds its capacity to regenerate, then eventually reductions in timber yield will lower the economic incentives for maintaining the concession. Under these circumstances there is a significant risk that the concession could be converted to a more profitable land-use such as agriculture or pastural lands. This would result in the degradation and clearing of a far higher percentage of the original forest than found in even the most exploitative of selective logging operations. Inevitably such a landscape transformation would equate with a substantial loss of forest dependent biota, including many of the bird species found within the La Chonta concession.

Chapter 4 provided the results of wet season bird surveys conducted in the La Chonta concession in 2003/2004. During point count surveys, I identified 5 062 birds, belonging to 155 species, and 33 families. Avian species richness was virtually identical between the reduced-impact logged and unlogged areas of the La Chonta forestry concession. Despite similarity in overall richness indices, one-third of birds were restricted to either the harvested, or unharvested areas of the concession (Chapter 5). Furthermore, twenty percent of all species were exclusive to, or significantly more abundant in, the unlogged areas of the concession. Members of the insectivorous and frugivorous avian guilds, as well as forest falcons, appeared to be disproportionately sensitive to the disturbance pressures associated with RIL (Chapter 5). I hypothesized that these differences in bird community composition result from several RIL related changes to forest structure, including: sensitivity to altered microclimate (eg. *Formicarius analis*); morphological limitations restricting a species ability to adapt to the vegetation types promoted by logging related disturbace (eg. *Micrastur ruficollis*); and the harvesting of timber tree species that are important fruit resources for large avian frugivores (eg. *Ramphastos vitellinus* & *R. tucanus*).

Chapter 6 demonstrated that bird community composition of logging gaps significantly differed from that found within natural tree-fall gaps in the unlogged forest. Two potentially synergistic causal processes were considered to be driving these differences. First, fundamental differences in the type of habitat created by natural and anthropogenic gaps may be attracting/maintaining different avian assemblages. For instance, anthropogenic gaps were significantly larger than their natural counterparts and differed in terms of the composition of regenerating vegetation (Chapter 2). Differences between anthropogenic and natural tree-fall gaps in terms of micro-climate and vegetation structure may be sufficient to cause the observed differences in the associated bird communities. Concomitantly, anthropogenic disturbance pressures appear to be reducing the abundance of some bird species throughout the harvested areas of the concession (Chapter 5). Several of these species (eg. channel-billed toucan, red-necked woodpecker) have niche requirements that extend well beyond the spatial scale and habitat types found within logging gaps. For these species, their reduced abundance within logging gaps is more likely to be related to processes operating throughout the concession than to processes limited to the the conditions experienced within gaps.

The motivation for forestry management to rectify the causal processes behind differences between anthropogenic and natural disturbance processes may be limited if the impacts are considered isolated to changes in bird composition. However, in Chapter 2, I suggest that current silvicultural practices (specifically the harvesting of *Ficus boliviana*) are creating very large gaps with microclimatic conditions preferentially beneficial to the regeneration of non-commercial pioneer species. It is therefore possible that adjustment to harvesting practices that would improve the regeneration rates of commercially valuable tree species, may also benefit forest-dependent birds. I suggest this because the same altered microclimatic conditions that disadvantage the regeneration of some commerical tree species, also appear to be unfavourable to some forest-dependent avian taxa.

The fact remains, however, that changes to bird community composition cannot be isolated from issues relating to the long-term sustainability of the forestry concession. For example, the significantly lower abundance of frugivorous toucan species within the harvested areas of the concession may eventually lead to altered patterns of forest regeneration within the concession. The decline of frugivorous toucan species may (in part) be tied to the harvesting of the free standing fig species *Ficus boliviana*. The harvesting of this tree species is disproportionately contributing to canopy discontinuity (Chapter 2), and potentially removing a valuable keystone fruit resource for the forest's frugivorous species (Chapter 5). Harvesting *Ficus boliviana* may therefore be reducing fruit availability especially during periods of overall fruit scarcity.

Toucans are more effective than smaller frugivorous birds at dispersing seeds to areas where the seeds experience lower rates of mortality (Chapter 5). This, in combination with the fact that several of the most important fruit sources for the frugivorous birds in this forest are commercial timber species, leads me to conclude that a significant reduction in toucan numbers could have serious secondary effects on the ecology of the forest. For these reasons, the true long-term costs and benefits of harvesting the free standing fig species *Ficus boliviana*, and other animal dispersed timber species (eg. *Spondias mombin*, *Pseudolmedia laevis*, *Pouteria nemorosa*) need to be carefully considered.

7.1 Concluding statement

Even if human disturbance regimes employed by an individual forestry concession are within the bounds of natural disturbance, it would take decades of research encompassing several harvesting cycles to suggest with any confidence that the forestry operation was ecologically sustainable. Nevertheless, there is currently active promotion of claims that RIL procedures applied within FSC certified concessions “conserve forest biodiversity” (FSC 2006) and are “environmentally responsible” (WWF 2006). In comparison to the impacts of conventional selective logging practices in the tropics, these statements may be considered reasonable. However, these claims are as yet unsubstantiated, with potentially serious repercussions if incorrect. First, unrealistic expectations regarding the biodiversity value of forests logged using RIL techniques could result in RIL entering fragile and biodiverse ecosystems where logging should be excluded. Second, these views could provide a misleading perspective regarding the contribution that RIL is making to counteract the loss of biodiversity from large areas of tropical forest. If we are to apply a precautionary approach, then the promotion of RIL may be warranted, as long as such promotion is limited to those areas already set aside for selective logging.

Ludwig et al. (1993) stated that “resource management is a discipline whose history is replete with spectacular failures, but whose practitioners seldom change their policies in response to past experience.” The development of RIL and certified forestry has the potential to be a reversal of this trend. There is increasing evidence that reduced-impact logging of tropical forests causes less damage to forest structure in the tropics than conventional selective logging techniques. Furthermore, prohibitions on hunting are laudable improvements that contribute to the conservation of birds and mammals of this and other certified forestry concessions. However, achieving such dramatic improvements relative to the exploitive nature of conventional selective logging can come with the risk of complacency. Despite these improvements, there is as yet insufficient data to suggest that RIL is a panacea for combining the need for forest products with the need to maintain those ecosystems that provide them. With more knowledge, and strong links between science and policy, there is a possibility that necessary adjustments can be made, and RIL can be seen as the first step towards the difficult and complex goal of achieving ecologically sustainable forestry in the tropics.

7.3 Limitations of this study

Although I believe that the conclusions reached at the end of each chapter are commensurate with the chapter's results, it is prudent to highlight some of the overall limitations of this study. First, the conclusions from this thesis are based on studies conducted within one certified RIL concession. It is currently unknown to what extent my findings are applicable to other tropical forestry concessions that employ RIL practices. Second, relative to the time-scale over which forest regeneration takes place, this study was limited to quantifying differences between unharvested and harvested areas four years subsequent to logging. It is unknown whether my results are indicative of future trends in either the trajectory of forest regeneration or bird community composition. Any statements in such regard can only be seen as speculative. Third, although bird surveys took place during the annual peak in avian activity, such concentrated surveys left seasonal variation in bird abundance unaccounted for. It is currently unknown whether bird community structure within the harvested and unharvested areas of the concession are similar throughout the year. Fourth, the processes that are hypothesized to be driving observed differences between the harvested and unharvested areas of the concession were untested. We expect that this, and the other limitations of this study, will be rectified by future research.

7.4 Key areas for future work

The following are key areas for future research that relate directly to issues raised in this thesis:

- Research is needed to quantify the damage from each component of the felling and bole removal process caused to commercial tree species in advanced stages of regeneration. The answers provided can guide policy decisions regarding how best to minimize those activities which may be contributing to current inadequate levels of regeneration for commercial tree species.
- Research is needed to determine whether bird species found at lower abundance within the harvested areas of this concession are declining within the harvested areas of other Neotropical RIL concessions. Replication of our results would suggest that uniform changes to RIL procedures may be possible to reddress the decline for some bird species within RIL concessions.
- Research is needed to identify the causal processes driving differences in bird communities within the harvested and unharvested areas of RIL concessions. Isolating causal processes will enable researchers to refine ways in which RIL practices can be modified to limit the loss of these vulnerable bird species.

The following are key areas for future research that are indirectly relevant to issues raised in this thesis.

- I observed trees being extracted from logging blocks officially harvested during the previous year. The re-entry into recovering skid trails using logging machinery damages or destroys regenerating vegetation. Because currently prescribed rotation periods (~25 years) are considered inadequate for the regeneration of commercial timber species (Pariona et al., 2003; Dauber et al., 2005), this practice of re-entering old logging blocks can only serve to exacerbate the problem. The extent of this practice needs to be quantified in this and other RIL concessions, and possibly eradicated.
- Forest workers in La Chonta consume meat from cattle raised on pasture land owned by Agroindustria Forestal La Chonta Ltd., and located adjacent to the forestry concession. During my research I was informed by a forestry worker that the proximity of cattle to the forestry concession is enticing jaguars (*Panthera onca*) out of the forest and into the adjacent pastural areas where several have reportedly been shot. Assessment needs to be made if this

anecdotal report is true, and if so, the impact of this practice on the concession’s jaguar population. Actions could then be taken to reduce both jaguar losses and associated cattle mortality. As hunting is not permitted in many certified forestry concessions, it is possible that other similarly controlled concessions in the tropics are using adjacent pastoral lands for meat production, with potentially similar repercussions for jaguars.

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White-bearded hermit (Phaethornis hispidus)

Photo by Adam Felton

Appendix 1

THE DISPLAY OF A REDDISH HERMIT (*PHAETHORNIS RUBER*) IN A LOWLAND RAINFOREST, BOLIVIA.

Citation: Felton, A., Felton, A.M., and Lindenmayer, D. B. A note on the display of a reddish hermit (Phaethornis ruber) in a lowland rainforest, Bolivia. Wilson Journal of Ornithology – Accepted July 2007

A1.1. Introduction

The Reddish Hermit (Phaethornis ruber) is a common inhabitant of tropical forest understory from Venezuela to south-east Brazil and is one of the smallest (~2.4 gm) known hummingbird species (Oniki 1996). Like many hummingbirds, Reddish Hermits form leks where several males display to females which visit these assemblages to choose a mate (Snow 1973). The displays of Reddish Hermits at leks and in captivity often involve visually spectacular and elaborate aerial manoeuvers (Mobbs 1971).

Davis (1934:732) observed the display of a Reddish Hermit in October 1931and suggested that it “must be seen for its beauty to be appreciated”. Over the ensuing decades, several researchers have provided written accounts of Reddish Hermit displays in the wild (Snow 1973) and in captivity (Mobbs 1971). One of these accounts (Snow 1973:171) describes a display performed by a visiting male in front of a territorial male within a lek. The visiting male is described as hovering “8-10 cm above and in front of the owning male” and, as it hovered, “the bird’s rear swayed side to side by about an inch while the head remained stationary”. Our objective in this paper is to provide the first detailed description, with supporting illustrations, of what appears to be a similar but more extensive display, which we suggest was by a male intruding into the territory of a neighboring male.

A1.2. Observations

One of us (AF) was conducting bird surveys on 23 August 2004 within the lowland subtropical humid forest (Holdridge Life Zone System) of the Guarayos Forest Reserve, Departmento Santa Cruz, Bolivia. This concession is ~300 km north of the lowland city of Santa Cruz. The forest varies in altitude from 230 to 390 m with an average elevation of 320 m. The mean annual temperature is 25° C with mean annual precipitation of ~156 cm. The region experiences a distinct dry season from May to October. One survey point was in a 471 m^2 logging gap (15° 40´ 07 S, 62° 45´ 77 W) created by felling a 60-cm dbh tower tree (*Schizolobium parahyba*; Caesalpiniaceae).

The following observations and sound recording were made in the understory of adjacent pioneer vegetation of two Reddish Hermits at 0620 hrs. The temperature was 14° C with 100% cloud cover and no wind. No conspecifics were noted within the vicinity during these displays, but the observed situation is not inconsistent with the circumstances expected to be found within a lek (Snow 1973).

We observed an individual *P. ruber* perched on a branch ~1 m above ground. The perching individual would flick its tail up and down, and occasionally fly to a different perch briefly during the displays of the other individual before returning to the original perch (Fig. 1). The displaying conspecific engaged in an intricate flying display ~25 cm to the front and above the perched individual.

A1.2.1 Rotation display

We refer to the first display as the “rotation display” (Fig. 1). The displaying individual conspicuously erected white plumage near its flanks, presumably of its thigh feathers. With its back arched and head raised, the bird increased its stroke amplitude to what we perceived was the point of contact (Altshuler and Dudley 2003), due to an accompanying continuous rapid droning sound, which was distinct from that produced during normal flight. We were under the impression that the wings collided at both the ends of the upstroke and the downstroke. The tail was simultaneously raised and lowered with a speed that blurred its image to the human eye. Concurrently the bird yawed through 300° of movement. This was one of the most mesmerizing aspects of the display due to the individual's capacity to avoid any corresponding rolling, pitching, or translational movement. This was done in a punctuated movement (at the start and end point of each arc), taking approximately 1 sec to complete an arc. At the same time, it rhythmically opened and closed its bill, thereby displaying the vibrant yellow coloration of the gape. All of these movements were characterized by extreme speed and precision and continued in repeated bouts that ranged from 3 seconds to over 75 seconds (mean = 15.4 seconds; n=15).

The rotation display was accompanied by a high pitch repetitious song that was made by either the displaying individual or the perched individual. Like Mobbs (1971), we do not feel confident categorically assigning the song to one individual or the other. It consisted of high pitched ascending and descending individual notes and trills (zee'zee'zee'zeezezezeze'zee), similar as that described by Nicholson (1931) as heard from a *P. ruber* lek in northern Guyana.

A1.2.2 Arc display

The individual at times switched to alternate, but equally transfixing behavior between rotation displays, which we refer to as the "arc display" (Fig. 2). The displaying individual during this phase remained facing the perched individual and moved laterally over a ~ 100° arc, as if tethered at the chest to its perching audience. Tail movements may have been related more to controlling flight, than to display. We estimate the amplitude (horizontal distance moved) of this display was ~ 30 cm. The displaying individual could complete 3 arcs within 1 sec with each arc punctuated by a "diu" call (Fig. 3). This call was consistently between ~1000 and 2000 kHz, inconsistent with the frequency of their normal "tsi" call. The arc display was flanked both before and after by the rotation display, and was the shorter of the two displays. The arc display ranged from 1.0 to just over 3.3 sec in length (mean =

2.0 sec, n = 8). The entire display ended suddenly with both individuals moving from the field of view. We are uncertain whether one chased the other away.

A1.3. Conclusion

We have several reasons for suggesting that both individuals were males and this observation was an antagonistic display similar to that described by Snow (1973). Among the hummingbirds, the hermits (Phaethorninae) are notable for their lack of sexually dimorphic characteristics (Höglund 1989). However, it is possible to use plumage characteristics for distinguishing male P. ruber from females (Höglund 1989). Both male and female P. ruber have a rufous breast, but the male’s breast is marked by a black ‘V’, with the female lacking this mark altogether or possessing an obscure black blemish in its place (Davis 1958, Oniki 1970, Höglund 1989). Both the displaying and the perched individuals in our observations had a black ‘V’. We are confident that both individuals were males and the observed behavior was not a courtship display.

Notably, it was the individual with the stronger male coloration that was perched, with the displaying individual’s black chest bar fainter. This may indicate the displaying individual was a less mature male. This would be concordant with the description by Snow (1973) of a male attempting to displace a more established neighboring territorial owner.

The other indication this display represents antagonistic behavior between two males over what appears to be lek territory is the season in which the observation occurred. Breeding records for P. ruber in this region of Bolivia are absent, but records from Brazil (Oniki 1970), Guyana (Davis 1934, Davis 1958), and Trinidad (Snow 1973) consistently show the breeding season overlaps with the local dry season. The observed display occurred during the middle of the dry season in this region of Bolivia and we are confident this was a breeding-related display.

We believe the most parsimonious explanation for the observed behavior is that it consisted of an encounter between a resident (perching individual) and intruding (displaying) male within what was likely a lek territory. We suggest that more systematic observations are needed before we can gain a thorough understanding of these intricate displays.

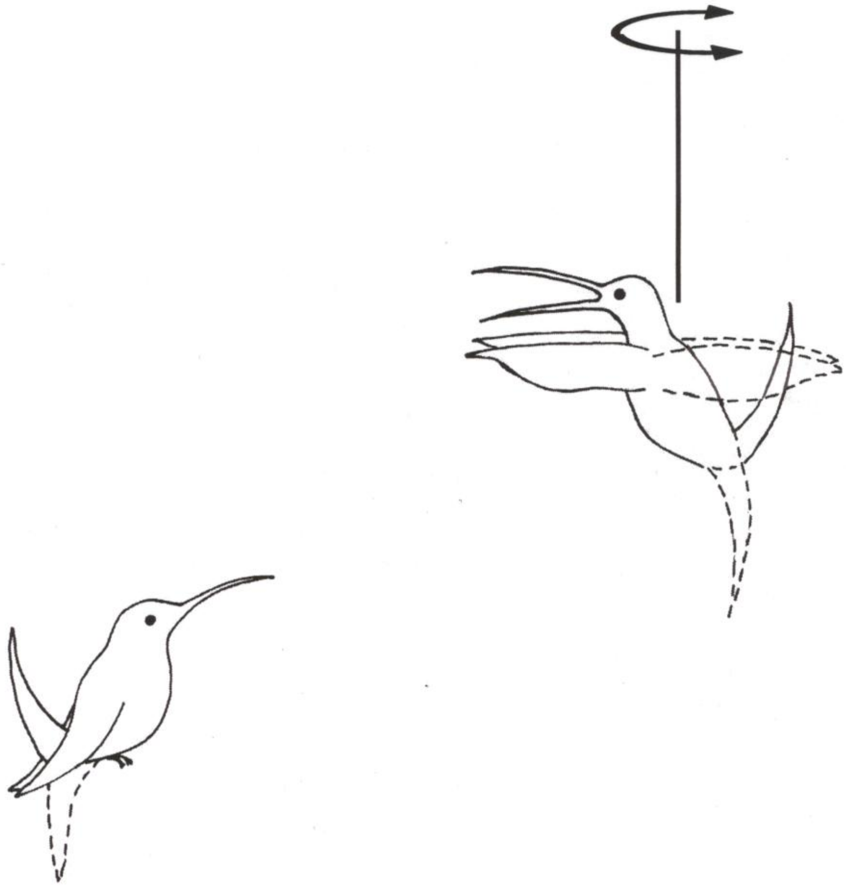

Figure A1.2.1. Illustration of the rotation display of the Reddish Hermit with the perched individual to the left and the displaying individual to the right.

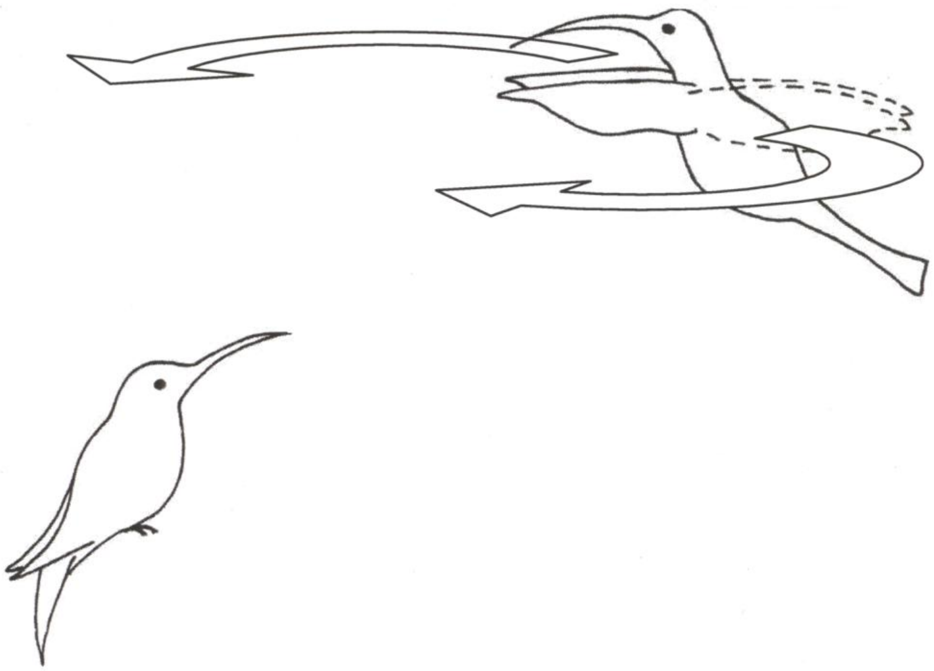

Figure A1.2.2. Illustration of the arc display of the Reddish Hermit with the perched individual to the left and displaying individual to the right.

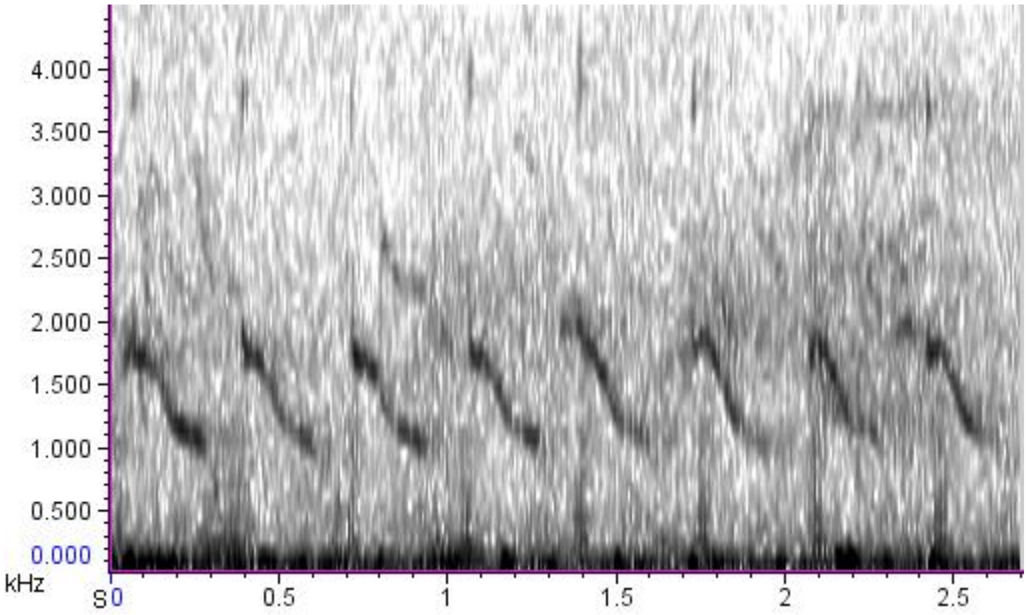

Figure A1.2.3. Spectrogram of "diu" sounds made by Reddish Hermit while performing the arc display.

A.3. Acknowledgments

This project was supported through the generous financial assistance of the American Ornithology Union, Sennheiser Australia, and the Lincoln Park Zoo. We thank the personnel of IBIF, Agroindustria Forestal La Chonta Ltd., Proyecto de Manejo Forestal Sostenible (BOLFOR), and Birdlife Bolivia (Armonia) for providing logistical support, especially Marielos Peña and Todd Fredericksen. Eugenio Mercado provided integral assistance during all phases of the field work and the advice of Ross Cunningham greatly contributed to the design of this project. Finally, we thank the Australian Red Cross without whom this project could not have been completed. All research was approved by the relevant authorities and this study was conducted within the ethical guidelines of Australia and Bolivia.

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Appendix 2

MAP OF BOLIVIA WITH APPROXIMATE LOCATION OF STUDY SITE AND PHOTOGRAPHS OF THE LA CHONTA CONCESSION

This appendix contains a map of the location of the study site used in the thesis and a schematic diagram of the sampling design. It also contains colour photographs that the reader may find helpful to visualise the vegetation types under investigation in this thesis.

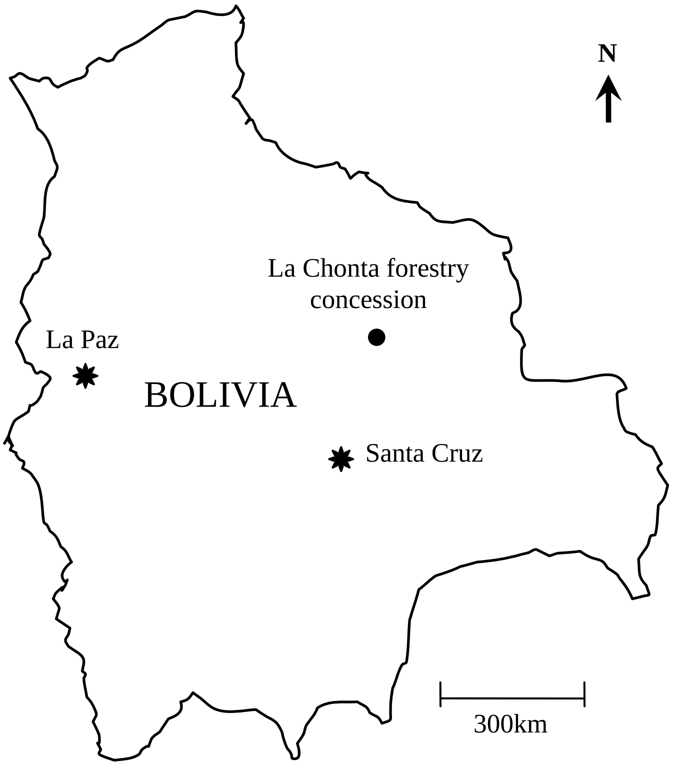

Figure A2.1. Map of Bolivia with approximate location of the La Chonta forestry concession indicated within the department of Santa Cruz, Bolivia. The La Chonta concession is approximately 300 km north of the lowland capitol city Santa Cruz.

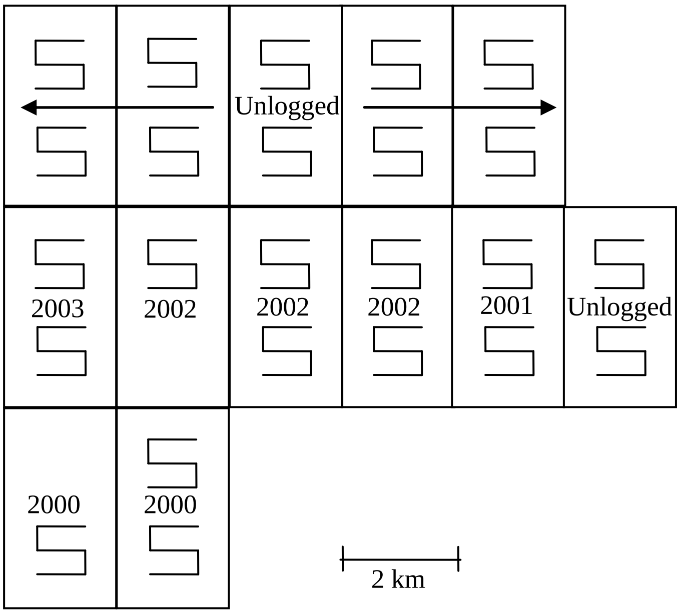

Figure A2.2. Schematic diagram representing relative location of reduced-impact logged blocks (labeled with year of harvest) and unlogged sites used in this study within the La Chonta concession, department of Santa Cruz, Bolivia. The 'S' symbol represents transects cut within each block. Five points, comprising one representative of each of the five vegetation categories, was place along each of three east/west transects of each 'S'. The east/west transects are ~1 km in length. Unlogged areas are to be harvested between 2004 and 2007.

Photo by Petter König

Camp Los Monos' main research building as seen pre-dawn and prior to hiking off to commence bird surveys.

Photo by Nadina Beck

Camp Los Monos shrouded in smoke as seen prior to commencing evacuation due to approaching forest fires.