Structure and diversity of cloud forest bird communities in Alta Verapaz, Guatemala, and implications for conservation

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Abbreviations

BM	body mass [g]
S	species numbers
N	individuals numbers
c	mist-net captures (marked individuals)
r	recaptures
R^t	recapture rate
DBH	diameter at breast height
UTD	understory tree density [m]
UTH	understory tree height [m]
UTS	understory tree size [m]
OTD	overstory tree density [m]
OTH	overstory tree height [m]
OTS	overstory tree size [m]
ha	hectare (1 ha = 10,000 m^2 = 0.1 km^2)
NF	natural forest
YSF	young secondary forest

Guatemala belongs to the Mexican Time Zone (UTC/WTC – 6:00 h) and has no time shift during summer.

1 Introduction

Biological diversity, at least in terms of species richness, is distributed unequally around the Earth (e.g., Mittermeier *et al*. 1998, Myers *et al*. 2000, Barthlott & Winger 2001). The majority of species is located in tropical regions, many in special habitats like mountain cloud forest or coral reefs (Primack 1993). More than 50 % of species occur within 7 % of land cover (Whitmore 1990, Conservation International 1990). Higher vertebrates and vascular plants show a higher frequency of species in the 25 terrestrial Biodiversity Hotspots, which are located mainly within the tropics, some reaching subtropical areas (Myers *et al*. 2000).

Parallel to the high level of biodiversity, there is a high degree of habitat loss in the same hotspot regions (Stattersfield *et al*. 1998, Myers *et al*. 2000). Deforestation is one of the major factors (Tanner *et al*. 1996, FAO 2001). 'Contemporary human activities is the latest chapter in a long saga of disturbances […]' and the most threatening (Whitemore & Burslem 1996). Fragmentation, degradation, and complete habitat loss are diminishing the natural forests. Species specialized to natural forests will vanish after a relaxation time when area is too small (e.g., Brooks *et al*. 1999).

The extinction of species as a consequence of habitat loss is leading to biodiversity loss, in temperate landscapes as well as in the tropics (e.g., Myers *et al*. 2000). Conservation and preservation of natural habitats is essential to preserve a high degree of biological diversity (e.g., Hughes *et al*. 2002).

The exact order of magnitude of species numbers is not known to the scientific community (Primack 1993, and others). There are several estimations of species numbers (e.g., Cox & Moore 2000). Taxonomists estimate that the majority of invertebrate species are yet undiscovered. For instance, insects are believed to be known to scientists with less than 10 % of all species (e.g., Cox & Moore 2000, Primack 1993). For other arthropods or invertebrates, the situation might be even worse (Wilson 1992). Numbers for higher vertebrates like birds are relatively constant and annual descriptions of new species are comparatively low (e.g., del Hoyo *et al*. 1992).

Deforestation and loss of natural habitats are the result of human activities. Rural human populations are reduced to basic and subsistence agricultures to obtain sufficient food for survival (Terborgh 1999, World Bank 2001). Traditional knowledge and increasing human populations force contemporary and future generations to continue or even increase deforestation to provide sufficient area for agriculture and land use. Inappropriate use and overexploitation of land makes it necessary to move on and exploit new areas, leaving vast unproductive areas (Markussen 2003).

While most species are still unknown, deforestation rates and human impacts are still increasing (e.g., FAO 2001, World Bank 2001). Hence biologists with their long-term studies are documenting the *status quo* of the remaining natural environments (Terborgh 1999).

Habitat loss and degradation often interact with scientific investigations and prevent surveys or falsify results. In contrast to increasing biodiversity research (mainly the socio-economic part), patterns and processes of biodiversity loss are still poorly known (Loreau *et al*. 2002). Community ecology focuses on "factors of biodiversity", while ecosystem ecology focuses on rates, dynamics, stability of energy and nutrition cycles (Naeem *et al*. 2002). Here, the focus is on the first part, i.e. community and diversity. Different ecosystem processes respond differently to biodiversity loss (Naeem *et al*. 1994, Naeem *et al*. 2002).

Studies involving standardized and comparable bird community measures in the tropics are rare (Terborgh *et al*. 1990). Studies estimating the impact of human activities on nature and its functioning are even more rare (Terborgh 1999). Worldwide there are less then 10 study plots with a more or less completely censused bird species inventory for an approximate area of 100 ha (Brosset & Erard 1986, Thiollay 1994a, Robinson *et al*. 2000, Waltert 2000). For other animal groups like mammals or insects, the situation is even worse.

Deforestation as the major impact on habitat loss in the tropics (FAO 2001) is threatening all kinds of species but especially highly mobile and top predator species, including many bird or mammal species (e.g., Begon *et al.* 1996). The influence of forest loss and fragmentation on species loss should be predictibale on the basis of species-area relationships (Magurran 1988, Rosenzweig 1995, Brooks *et al*. 1999a). Reduced forest areas cannot support the same number of forest birds as larger areas. However, smaller forest fragments are inhabited by fewer species than expected by a linear species-area relationship (e.g., Rosenzweig 1995). Like the top predators, other forest specialists and endemics will vanish (Stattersfield *et al*. 1998) from fragments due to decreasing size and numbers of forest fragments (MacArthur & Wilson 1967, Greenberg 1996, Kattan & Alvarez-Lopéz 1996, and others).

Neotropical montane cloud forests and their endemic birds are greatly threatened (Veblen 1976, FAO 2001, Kappelle & Brown 2001, World Bank 2001). According to FAO (2001), highland forests in Guatemala have a higher deforestation rate than lowland forests (0.8 % versus 1.1 % annually between 1981 and 1990). Many Endemic Bird Areas (EBAs after Stattersfield *et al*. 1998; Long 1995) are located within cloud forests and therefore are threatened by recent human activities.

Veblen stated in 1976 that the conservation of forests in highland Guatemala is necessary because many pine species are present above average in the region and diversity is high. Natural montane cloud forests were reduced substantially to one third of their original extent in Guatemala and highly fragmentized in 1988 (Mühlenberg *et al*. 1989)

The influence of forest changes (from natural to secondary forest) on diversity has rarely been invetsigated within tropical landscapes. Terborgh & Weske (1969) showed that natural forest has more species than secondary habitats in Amazonia. Lawton & May (1995) assumed that few tropical forest animals and plants will survive in agricultural landscapes.

Hughes *et al*. (2002) found fewer species of birds in tropical secondary forests than in natural habitats. Nevertheless, they concluded that this might not be valid for all habitats in general.

In the present study the bird community of a Neotropical montane cloud forest in central Guatemala was described, with emphasis on the differences between natural and human-induced habitats. I attempted to answer the question whether or not secondary habitats have a similar degree of avian diversity as natural forests. Locally extinct species were identified, and predictions of further extinctions made. Finally, the necessity and consequences for conservation strategies were explained.

A 102 ha study plot was established with emphasis on the two major habitat types: natural forest (near primary) and secondary forest (approximately 5 years old), both habitats representing half of the study plot. Within each habitat type, species richness, heterogeneity, evenness, abundance and total and individual body mass distribution were analyzed to evaluate the habitat quality of natural forest compared to young secondary forest for the bird community.

2 Background

This study is part of the interdisciplinary graduate student training program (“Graduiertenkolleg” or GK) of the Deutsche Forschungsgemeinschaft DFG entitled “Evaluation and Conservation of Biodiversity”. The GK was installed to educate German scientists in biodiversity research, because there was and still is a shortage of scientists, especially non-natural scientists, involved in biodiversity research.

Biodiversity, introduced by Wilson into the biological sciences in 1988, is the diversity and variability of life and living organisms and their ecological structures (Wilson 1988, Primack 1993, Gaston 1996, and others). Based on the same definition, The Convention on Biological Diversity (CBD, Rio de Janeiro 1992) is an international convention with the aim of preserving biodiversity. The term “biodiversity” was originally used in organismic biology as species richness but nowadays is used in many different ways to investigate and preserve nature. The definition has changed so that the term biodiversity might be used in any topic related to nature. This change is projected in parts of the GK too. The majority of the projects dealt with economic and/or social aspects of biodiversity and its applications.

The present work is related to the CBD by Article 7 “Identification and Monitoring”. With respect to Annex I of the CBD the purpose of the present work is to identify “1. Ecosystems and habitats: containing high diversity, large numbers of endemic or threatened species, or wilderness; …”, and later in part 2 “Species and communities which are: threatened; …”.

Montane cloud forests of the world are a highly endangered ecosystem or habitat type (Kappelle & Brown 2001, Doumenge *et al.* 1995). The investigation of this habitat in Guatemala with respect to the bird community is an important topic and research is needed. In tropical forests, standardized monitoring has been proposed (compare Terborgh *et al.* 1990) but has actually been carried out in only a few areas (Terborgh *et al*. 1990, Thiollay 1994a, 1994b, Robinson *et al.* 2000, Waltert 2000).

Most studies involved in conservation focus on one or at least few species, e.g., conspicuous species like *Pharomachrus mocinno* (Resplendent Quetzal) in Central America (e.g., Powell & Bjork 1994, 1995) or *Ailuropoda melanoleuca* (Giant Panda) in south-east Asia (Liu *et al*. 2001). The advantage of those surrogates is the wide acceptance and money-acquiring effect for conservation. But the effect of the single species approach is disputable.

Deforestation – or in general terms loss of natural habitats – is one of the major reasons for species extinction (Terborgh 1999, World Bank 2001, and others). Within the study area in the Sierra Yalijux the annual deforestation rate has decreased within the last ten years (David Unger, pers. comm., Voigt 2003, Markussen 2003). Nevertheless, due to the high degree of forest fragmentation and small total area of forest remnants, the forest still is affected by human impact. As in most reserves in Guatemala (e.g., Parque Nacional de la

Sierra de las Minas [Defensores de la Naturaleza 2001], Parque Nacional de la Laguna Lachuá), there is still random extraction of timber or creation of agricultural areas in the natural forest.

3 Objectives and hypotheses

Objectives of the study are

- to document the different habitat structures of the study plot landscape mosaic and the human influence on birds, mammals, and vegetation using different standardized methods;
- to document the diversity, composition, and structure of the forest bird community and highlight the differences with regard to natural and human-made habitats;
- to compare the study site with other studies in Central America and the Neotropics;
- to work out a conservation strategy to preserve the remaining natural forest and suggest necessary steps from a biological conservation viewpoint;
- to estimate the degree of threat to Central American highland endemics and natural forest specialists and analyze their population viability in the study area;
- to determine and explain the conservation problems in the Sierra Yalijux (small scale) and estimate the consequences of further deforestation.

Alongside the descriptive character of the study, the following hypotheses and questions will be tested and answered:

The remaining natural forest has lost species from its expected original species inventory. Several species are extinct or near to extinction, and more species will vanish due to fragmentation and natural habitat loss (Bierregaard 1990, Bierregaard & Stouffer 1997) even if deforestation were stopped now. The forest remnants are too small to carry the complete expected set of bird species. Larger carnivores and top predators in particular are absent from the study area (Terborgh 1999). The cloud forests are forest-archipelagos (Vásquez-García 1995) in an agricultural mosaic landscape. The species-area-equilibrium has not yet been reached (Rosenzweig 1995, Brooks *et al*. 1999a, 1999b, 1999c).

Natural forest and young secondary forest may differ in bird diversity, territoriality, endemism and/or biometrics, but these differences might be less pronounced then in richer bird communities of unfragmented forests. Most species present are either forest generalists or are also adapted to open country habitats.

Natural forest is not distinctive as an important reproductive source for species compared with young secondary forest. Natural forest is the state of the forest in its natural condition, i.e. here natural forest is considered to be (near) primary vegetation. Differences and distinctive aspects of young secondary forest are consequences of human impact on the natural vegetation. The diversity and structure of the bird community depends on human impact: secondary habitats have *per se* lower diversity and species richness than natural forest. Nevertheless, diversity and species richness in secondary habitats depend on the age and structure of the vegetation (Hughes *et al*. 2002).

Conventional analyses of bird diversity assessments using mist nets possibly influence data on species which are mainly distributed in natural forest's higher vegetation strata but are still present in young secondary forest habitats. Overstory species were censused using methods that do not influence analyses of diversity and species richness. Several true natural forest canopy species do not care if there are three or 30 m between them and the ground (Bierregaard & Stouffer 1997). This might affect the applied methods. Differences occurring in vertical stratification are worked out and consequences outlined for diversity indices concerning (i) the methods and (ii) vertical stratification and corresponding analyzes: Diversity, species richness, and evenness are not the same in both natural forest and secondary forest (H_0: There are no differences concerning the mentioned parameters between natural forest and secondary habitat). Understory bird communities are significantly influenced by human impact. Here the influence of human use in understory bird communities in natural forest and young secondary forest is tested. Based on diversity and trophic studies – the ecosystem and the community approach (Naeem *et al*. 2002) – the influence will be tested (H_0: Land use in general does not influence diversity).

For accurate analyses of the bird community it is normally assumed that all bird species are detected by the applied methods, i.e. mist netting censuses all species independent of (e.g.) vertical stratification. But especially different vertical stratification preferences in natural forest and young secondary forest emphasize the analyses of (i) the vertical distribution of each species in natural habitats and (ii) understory birds in all habitats without overstory or even canopy species (Waltert 2000). This prevents the effect that several species in natural forest are abundant exclusively or mainly in canopy/overstory, but in young secondary forest – with compressed strata or a single stratum – might be crowded in appropriate heights for mist nets.

The Chelemhá Plot is not comparable with other standardized plots in the Neotropics in terms of diversity, species richness, and abundance of birds. It is more likely to be similar to temperate or subtropical bird communities. It will be tested if diversity patterns in the study plot fit within general patterns of cloud forest and/or lowland rainforest in Central America, the Neotropics, or pan-tropically.

Bird species diversity is related to vegetation structure: Pearson (1975) and others state that bird diversity increases with increasing foliage complexity. Due to vegetation and habitat heterogeneity, abundance of the species involved is not homogeneous either (Hutchings *et al*. 2000). The bird community of forests is influenced even by the landscape matrix (Renjifo 2001).

The forest is not too small to carry viable populations of all species. *Pharomachrus mocinno* will lose its breeding holes with the vanishing natural forest. This will reduce the breeding success of the species. After a time lag the species will disappear from the study plot and from the Sierra Yalijux. The background question here is, whether the forest is suitable for the preservation of further populations of conservationally interesting species or are the remaining forest remnants unable to carry viable populations of (e.g.) *Pharomachrus mocinno* or others.

Last but not least, is secondary vegetation in the study plot suitable for preserving a comparable degree of diversity *sensu lato* as natural habitats?

4 Methods, material, and study area

4.1 *Study area*

Located in the center of Guatemala (Figure 1), the study area belongs to the faunal region of the Neotropics. The Neotropics include the South American continent and the Caribbean (Stotz *et al*. 1996).

The study plot is located in the higher elevations (1980 to 2550 m) of the Sierra Yalijux, Departamento Alta Verapaz, Guatemala (15° 22’ N, 90° 03’ W). It belongs to the community Chelemhá (sometimes written Chelemá; the Q’eqchi (Kekchi) meaning of che-lem-ha’ is: “Tree which is reflected in a lake”, probably referring to the Lago Izabal located approximately 50 km to the east), Municipalidad de Tucurú. The Sierra Yalijux is here referred to as the study area, the study plot (from now on Chelemhá Plot) is part of the study area.

In this chapter the natural conditions and the location of the study plot are described. Markussen (2003) describes the study area in more detail, especially soil conditions, climate, and relief. Voigt (2003) focuses on deforestation and land use in the study area.

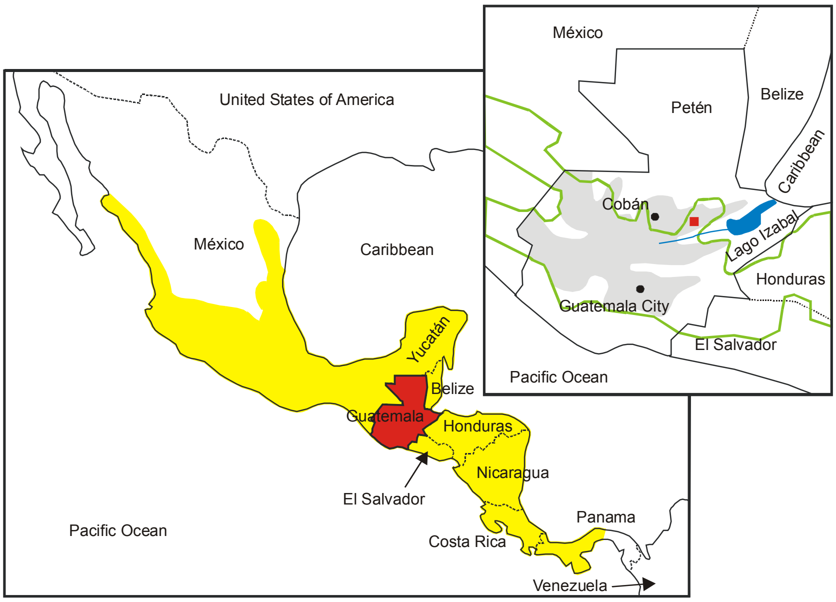

Figure 1: Location of Guatemala in Central America and the study area (Sierra Yalijux) in Guatemala (■). Yellow (■): biodiversity hotspot after Myers *et al.* (2000), gray in inset (■): elevation above 1000 m, green line (–): Endemic Bird Area (EBA # 018) after Stattersfield *et al.* (1998).

4.1.1 Topology and geology

Within the major mountain ranges of Guatemala, the Caribbean and the Coco tectonic plates move alongside each other (Zahn 1991). This has caused the folding of the central mountain ridges of Guatemala and the slopes descending to the northern (Petén, northern Guatemala) and southern (Pacific) lowlands. The central mountains are called the Central

American Highlands. The valley of the Río Polochic in the south of the study area is the border between the two tectonic plates. Earthquakes occur all year round.

The soil consists of Permian karst (Instituto Geografico Nacional 1997) and folding occurs to an elevation of about 2550 m. At several locations in the study area the karst is washed out by the high precipitation. Several dolines are present.

The slopes in the study area are in parts very steep and inclinations of 60° or more occur.

4.1.2 Climate

The study area belongs to the Central American highlands (Stotz *et al.* 1996, Stattersfield *et al.* 1998). The climate is tropical and the study plot belongs to the montane and submontane tropical rainforest (Holdridge 1967). The climate is tropical to subtropical depending on elevation and definition (Müller 1996). Following the classification of Thornwhite, the study area climate is humid and the natural vegetation forest. Holdridge's classification (1967) for Chelemhá is cold subtropical very (i.e. hyper) humid forest. Following Köppen's classification (*ex* MAGA 2001) the region is subtropical, with a cold and arid period and humid conditions most times of the year.

The central dry valley of the Río Montagua divides the northern and southern mountain ridges. Guatemala belongs to the tropics ($\geq$ 9 humid months, south of the Tropic of Cancer at 24°30' N). The northern and southern lowlands and highlands show typically high precipitation (up to 4000 mm p.a.). In the highlands, surrounded by mountains, is an all-year-round dry valley (Valle de Montagua, precipitation around 600 mm p.a.) with thorn and shrub vegetation.

The Sierra Yalijux is located in the northernmost mountain ridge above 2000 m of Guatemala and is the first major barrier for clouds moving southward over the Petén lowlands. This causes generally high levels of precipitation in the Sierra with regional differences: in the north-eastern part the precipitation is twice as high as in the south-western part of the mountain ridge (David Unger, pers. comm.). In the north-eastern parts the precipitation reaches 4000 mm p.a., 3604 mm between March and December 2002. Main wind directions are from east and north.

The climate is seasonal, with rainy season beginning in mid-May and ending in September/October. During August there is a two-week period with less rain, the so-called *canicula* or *veranillo*. Mist and rain in November and December is common. Relatively cold periods occur in January until March (the temperature may fall below 0 °C at night).

The temperature is relatively constant within the study plot during the year but changes diurnally (natural forest interior: annual minimum 1.6 °C, annual maximum 16.4 °C; monthly mean minimum 9.1 °C, monthly mean maximum 12.4 °C). Humidity is high during the day in natural forest and changes during the day in secondary vegetation (own data).

4.1.3 Natural vegetation

Tropical montane cloud forests are located between 500 and 3500 m altitude worldwide. Their major occurrence is between 1200 and 1500 m. The typical phenology of tropical montane cloud forests is the condensation of saturated humid air which results in clouds or mists in the forest.

During the last 40 years the natural vegetation cover has decreased steadily in Guatemala (FAO 2001, World Bank 2001). Natural forest cover is reduced to steep slopes and the high mountain ridges. During the last decade in particular the human population has steadily increased (World Bank 2001) and moved further into the forest remnants (Islebe & Véliz Pérez 2001). The mean annual deforestation rate in Guatemala is 1.7 %, which equals currently an area of approximately 50 000 ha of natural forest (FAO 2001, World Bank 2001).

The natural vegetation cover is still present in the study area and can be described as oak-pine cloud forest (Islebe & Véliz Pérez 2001). The overstory is dominated by *Quercus* sp. (*Quercus*-Lauraceae-cloud forest), while the understory is dominated by tree ferns (Cyatheaceae). Large open areas are rare, but many gaps occur with diameters extending up to 60 m. Pines are rare on the northern slopes but their abundance increases southwards until they are common on the southern slopes below 1000 m.

The natural forest is single- or multi-layered, depending on topology and microclimate. On the ridges there are mostly tall oaks with a high canopy (approximately 30 m). They are scattered with epiphytes (Bromeliaceae, Pteridophytes, Orchidaceae) which create habitats above ground (*Hängende Böden*, Schulz & Menzel 2000). The understory on the ridges is hardly developed. On the slopes there is a mixture between the different layers. The canopy of one tree may not exceed the nearby understory or midlevel of nearby trees even when the trees reach 30 m in height.

Typical for forests in the region are the high numbers of slowly rotting tree stumps. Some trees still look alive, but died several years ago and are simply covered with epiphytes. Often those tree stumps contain breeding cavities for birds like *Pharomachrus mocinno* (Unger 1988, chapters 5 and 6).

4.1.4 Habitat types of the Sierra Yalijux

There are two major types of habitat, natural forest and secondary growth. The latter is separable into at least three different types (old secondary forest, young secondary forest, and agricultures outside the forests) in the total study area, but within the study plot only young secondary forest is included in the study. Both natural forest and young secondary forest covered approximately 50 % of the study plot.

The natural forest is almost intact but nevertheless used by humans. The virgin-like forests are present at several locations but are used by people. The current use of the forest is confined to minimum hunting and timber extraction of small wood (diameter of stems 5 – 10 cm).

The natural forest canopy reaches heights between 25 and 35 m. Some few oaks reach a height of 40 m above the ground. Young secondary forest is mono-layered with a maximum height of 7 m and very dense. The visibility is below 2 m, defined as visibility of pure soil or soil covered with leaves. The natural forest remnants of approximately 55 km² (David Unger, pers. comm.) are surrounded by secondary vegetation patches. Between 1950 and 2000 natural forest cover decreased from 77.0 to 26.6 % in Guatemala. The current deforestation rate is 1.7 % (FAO 2001). Most deforestation is carried out in the northern lowlands of Guatemala (Petén). The deforestation rate in the study plot is considered to be less than the Guatemalan mean.

According to Levey's method (1988) there are mainly two stages of vegetation. Stage S1 (dense foliage at eye-levels low canopy) is frequent if it is considered that the "canopy" in 3 to 4-year-old secondary forest is between 3 and 5 m above the ground, which may not be called canopy. S1 is represented at 39.0 % of all points in the vegetation records. The second most frequent group (54.4 % of recorded points) is S3, i.e. high and multi-layered canopy with considerable foliage in all strata. The two classes GAP and S2 are represented with 4.4 % and 2.2 % respectively. The classes used by Levey (1988) are not suitable for the cloud forest region of Alta Verapaz, because neither the agricultural areas nor the vertical strata of the oak-pine forest are satisfactorily classified.

Most parts of the study area are used as *milpa*-system, i.e. corn fields (*Zea mays*, Poaceae). The patches are used for several years, sometimes nonstop since their creation in 1950 (Chicacnab, Manuel Chut, pers. comm.), and then are left for two or three years to recover (slash-and-burn agriculture). The vegetation is cut down and after a short drying period burned in late March. Until October the seeds grow up to a height of 4 m and the corn is harvested. Sometimes the corn is accompanied by beans. The structure is homogeneous. Bush and shrub vegetation (here referred to as young secondary forest) is the result of the recovery period of the slash-and-burn agriculture. Depending on age and recovery time, the bushes grow up to 4 m in height. Mostly fast-growing species dominate this habitat. The vegetation is very dense with visibilities below 1.5 m (at one year) and 3 m (4 years). The study focuses on this secondary vegetation type as it was possible to use an area without agricultural activities in a sufficient area close to the sampled natural forest. From now on it is referred to as young secondary forest.

All areas which have been logged, and have been without further human impact for more than 10 years, are classified as old secondary forest. The maximum tree height is 15 m. The vegetation is dense and there is only one layer. Fast-growing plant species are dominant.

This habitat type is rare at Chelemhá and is not included in the study. Bordering on the study plot, there is a small area of approximately 1.5 ha of ten-year-old secondary forest.

Pine reforestation areas are much like bush and shrub vegetation. The pines in Chelemhá (*Pinus maximinoii*) were planted at 3 m distances. Small bushes and thorny vegetation remain between the pines. A small area (less than 1 ha) of the young secondary forest was scattered with pines planted in 2000.

All secondary vegetation types mentioned form a mosaic-shaped landscape. Old secondary forest and *milpa*-system were not included in the study plot. Figure 5 illustrates a typical vegetation transect in the study area.

Young secondary forest has no vertical stratification, i.e. there is one relatively dense stratum. For practical reasons here it is referred to as understory, because it exceeds similar heights as understory in natural forest.

4.1.5 Fauna

There are hardly any studies concerning faunal research or community assessment at Chelemhá. Most studies focus on insects (Cano & Morón 1998, Mónzon Sierra *et al.* 1999, Schuster *et al.* 2000) and were carried out at various place in the Sierra Yalijux. Hauswirth (2003) summarizes the results of the arthropod research. Other invertebrates have not been studied in the Sierra Yalijux.

Most records of mammals are made by the locals and not confirmed by scientific records.

Concerning birds there is one study that was conducted in the nearby cloud forest of the Sierra Caquipec (Eisermann 2000). One hundred thirty-five different species were observed in Chicacnab, 12 km west of the study plot in Chelemhá. Eisermann (2000) used transects and sight records (Chapter 6.3). Further studies of bird communities were conducted in Panama (Robinson *et al.* 2000) and in the Sierra de las Minas approximately 30 km south of the study plot in Chelemhá at the end of 2003 by Andrea Nájera (pers. comm.). The latter study is still carried out at the printing of the thesis and results therefore were not compared.

4.2 Study plot

The study plot is located in the cloud forest area to the west of the buildings of the community of Chelemhá. Figure 1 shows the study plot location within Guatemala and Central America. The study plot is part of the study area in the Sierra Yalijux, Alta Verapaz.

The total area of the study plot is 102 ha, with a 52 % covering of natural forest and 48 % covering of young secondary forest. The planned area of the study plot covered by transect census techniques and mist netting (Chapter 4.4) was measured by GIS (Chapter 4.6) applying the method “buffering” along the transect and mist net lines.

The setting of the transects and mist net localities are described in the relevant sections below (4.4.1 and 4.4.2). In Figure 19 there is an overview of the altitudinal ranges, the forest edge and the approximate limits of the study plot. Figure 2 illustrates the approximate locations of the 12 mist net lines and the transects.

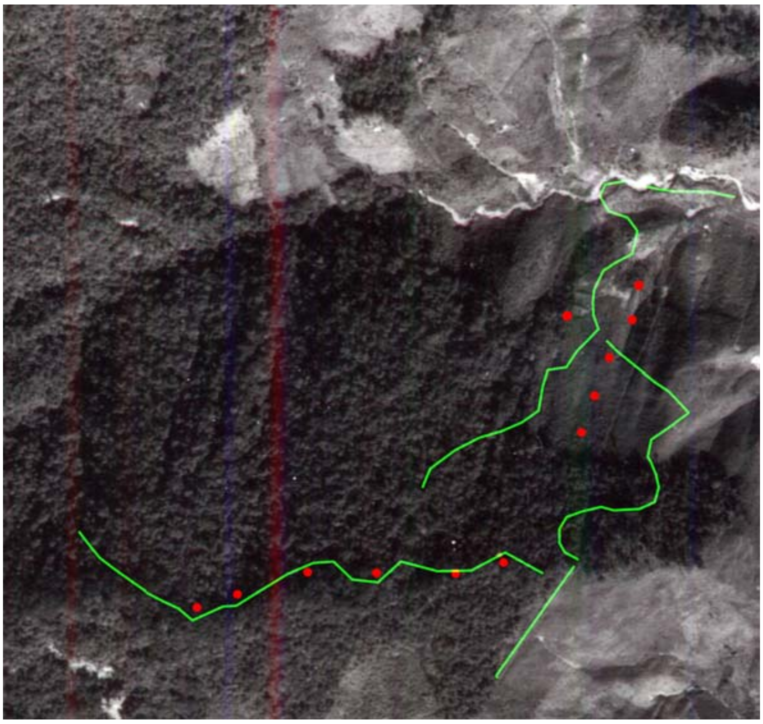

Figure 2: Aerial image of the study area from 20 January 2000 (detail from image # 0182, Instituto Geografico Nacional 2000). Natural forest is represented by the dark area, lighter gray parts are secondary habitats and human settlements of all kinds. Red dots (●) give the approximate location of each net line in the study plot, green lines (—) the approximate locations of the transects. Note: the latter are divided into 150 m sections which are not illustrated in the image.

4.2.1 Diameter at breast height (DBH)

In 2002 there were two foresters helping and advising in the determination of the natural forest structure of the study plot (Dölle 2003). Although they gathered data from young secondary forest, Dölle (2003) analyzed the vegetation structure of the study plot in Chelemhá from the viewpoint of a forester.

Altogether 82 trees were analyzed with regard to DBH, 50 in natural forest and 32 in young secondary forest. In Table 1 the classes are defined. Natural forest has DBH in all eight classes more or less equally distributed, while in young secondary forest the main class consists of diameters below 20 cm (Figure 3). The distribution shows the differences in age structure of the two habitats.

Table 1: Diameter at breast height (DBH) and tree height (TH) in Chelemhá. The classes are used for illustration in Figs. 3 and 4.

Class	DBH [cm]	Tree height [cm]
1	≤ 20	≤ 5
2	20 ≤ 40	5 ≤ 10
3	40 ≤ 60	10 ≤ 15
4	60 ≤ 80	15 ≤ 20
5	80 ≤ 100	20 ≤ 25
6	100 ≤ 120	25 ≤ 30
7	120 ≤ 140	30 ≤ 35
8	140 ≤ 160	35 ≤ 40
9	–	40 ≤ 45

4.2.2 Tree height

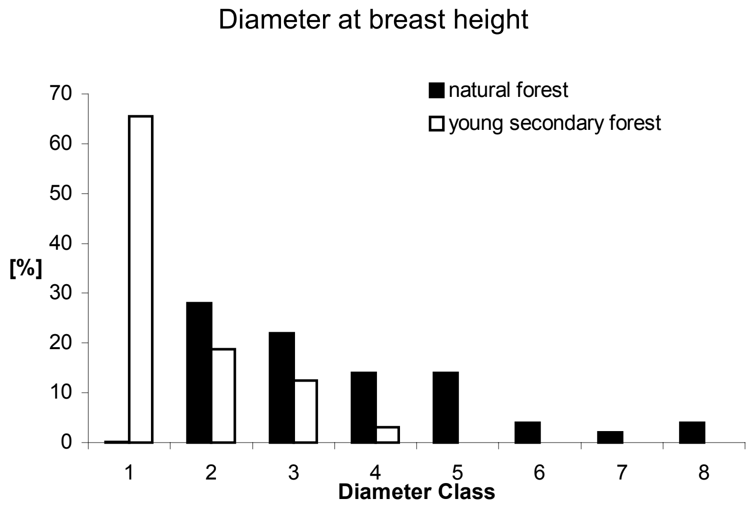

Figure 3: Distribution of diameter at breast height classes (DBH) in relative abundance in natural forest and young secondary forest in Chelemhá. Diameter classes are defined in Table 1. Redrawn from Dölle (2003).

A similar pattern to diameter at breast height is given by tree height distribution of the two vegetation types (for classification see Table 1). Trees above 25 m are not abundant in secondary vegetation, most of the trees being between 5 and 10 m (47 %). In natural forest the tree heights are more equally distributed, but there are two peaks of tree height (Figure 3): 5 to 10 m and 30 to 40 m. This indicates the mostly two-layered structure of the natural forest of the Sierra Yalijux (Dölle 2003).

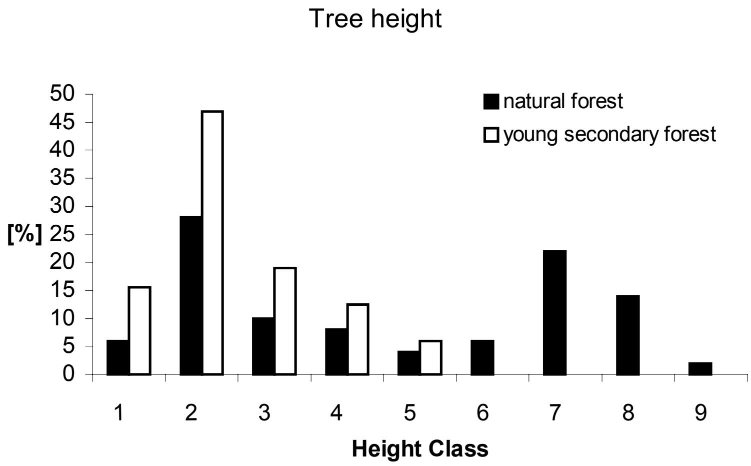

Figure 4: Distribution of tree height (TH) classes in relative abundance in natural forest and young secondary forest in Chelemhá. Height classes are defined in Table 1. Redrawn from Dölle (2003).

4.2.3 Tree stem cover

The coverage of tree stems with lianas, mosses, and epiphytes shows that secondary growth has hardly any associated plants on tree stems. In natural forest there is a clear dependent pattern between stem diameter and coverage, i.e. the larger the diameter (and older the tree) the greater the relative tree coverage (Dölle 2003).

4.3 Vegetation structure

Vegetation structure is an important factor for the presence or absence of birds (Levey 1998, Slater 1995, Waltert 2000, Whelan 2001, and others). Several methods were used to qualify and quantify the vegetation structure of the study plot.

Levey (1988) introduced a brief method to quantify the vegetation structure of primary forests with regard to birds in tropical areas. Levey (1988) distinguishes four stages of vegetation structure (Figure 5):

- GAP, a vertical hole in the vegetation down through all strata, canopy lacking;
- S1, with a single-layered canopy at low heights, dense foliage at eye-level;
- S2, with a single-layered canopy at low heights and sparser foliage at eye-level;
- S3, with a multi-layered canopy and considerable amounts of foliage in all strata.

To get a measure of the vegetation structure the understory and overstory trees were measured in different ways. To distinguish the overstory and the understory trees, the nearest trees at a given point (at each mist net and each 25 m transect point mark) with a diameter at breast height (DBH) above 20 cm were assigned to the overstory. The nearest trees with DBH between 2 and 10 cm were assigned to understory. Mid-levels were neglected because of being rare in the study plot and hardly distinguishable from the understory.

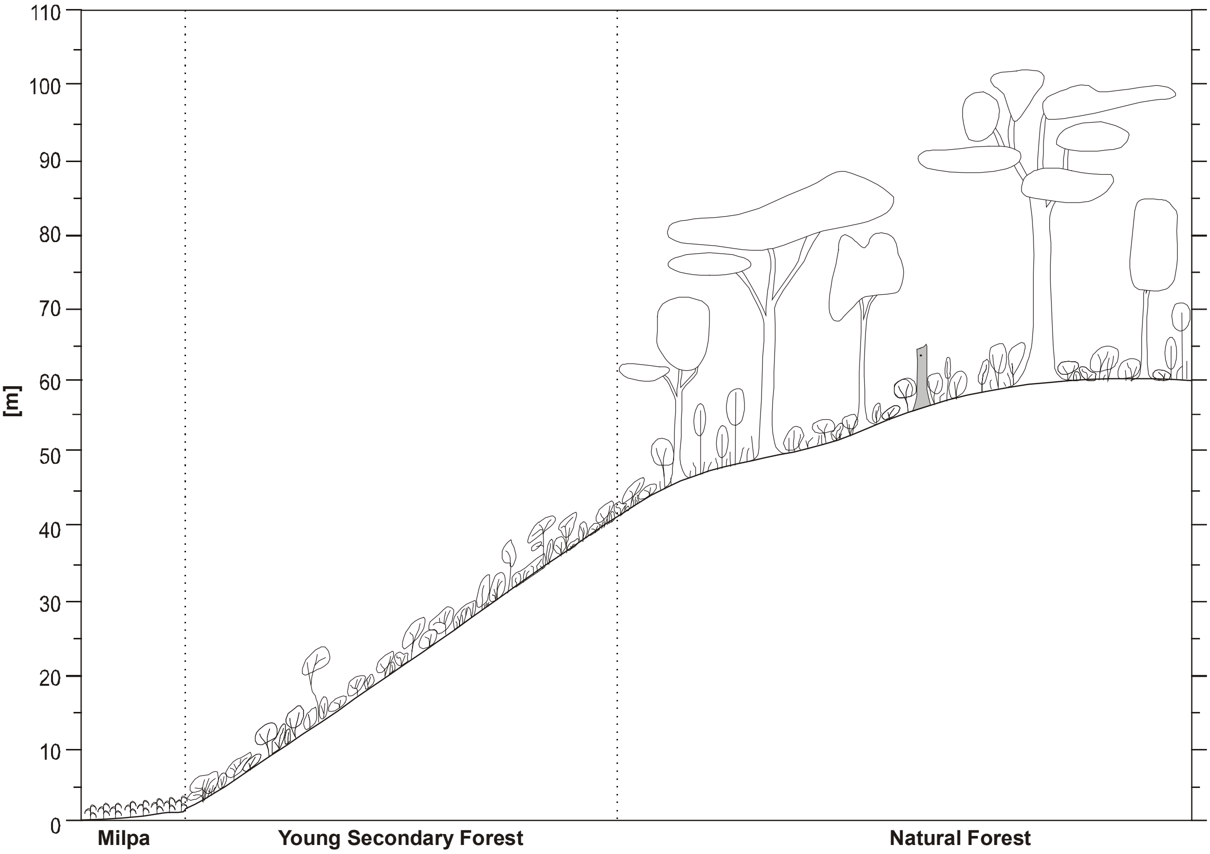

Figure 5: Morphological classification of succession stages based on structural characteristics of understory and canopy in Chelemhá. See chapter 4.3 for details. The gray tree is a rotten stump used by *Pharomachrus mocinno* for breeding.

Density of overstory (OTD) and understory (UTD) trees were taken at each point. Additionally, the estimated tree size at breast height (OTS and UTS respectively, resembles DBH) and the tree height (OTH and UTH respectively) were measured.

Deforestation and land use change were determined by analyzing aerial and satellite images (Instituto Geografico Nacional 1964, 1991, 2000; Landsat TM 14 April 1986, Landsat ETM 23 January 2000). For further details of the aerial image analysis see Voigt (2003) and Markussen (2003).

4.4 Ornithological fieldwork

Most species in the Sierra Yalijux breed from end of March to August – here referred to as the main breeding season. Nevertheless, several species breed all year (Howell & Webb 1995). The main study period therefore was from May to August 2001, and from March to August 2002. Because the study focuses on resident and breeding birds, this is the most important time of the year. Additionally, the study plot was visited in December 2001 to see if there were significant differences in species composition during the year. Neotropical and Nearctic migrants are excluded except for two species (see below) because they do not play such an important role and their frequency is low.

Birds were recorded by two different standardized methods: mist netting (Chapter 4.4.1) and transect census counts (Chapter 4.4.2). Both methods record species differently (e.g., Bierregaard & Stouffer 1997, Karr 1981, Remsen & Good 1996). The first determines recapture rates and changes in individual body mass. The latter is useful for determining abundance and species richness. Finally, all coincidental records were noted daily and integrated to complete the species list of residents not included by the other two methods.

4.4.1 Mist netting

Regarding those birds which are either marked by low calling activity or mainly live below 2.5 m, i.e. the net height, it is useful to capture them by mist nets. For further discussion see Bierregaard & Stouffer (1997), Waltert (2000), and Chapter 6.1.

In 2001 and 2002 the mist nets were opened on 78 days for a total of 5304 hours per net (each net is 12 m, i.e. 63 648 net meter hours were conducted, Table 2). On each day the mist nets (eight in each net line with 12 x 2.5 m) were opened between 06:00 h and 14:30 h. Each net line was opened six times, two days in 2001 and four days in 2002.

A total of 12 net lines were established in Chelemhá. Each of the two habitats (natural forest and young secondary forest) were netted with six net lines, distributed over an area of 21 ha, with a distance of 150 m between and 50 m to each side of the nets.

All captured individuals were sexed and aged, as far as plumage patterns or morphometrics allowed differentiation. Species determination followed Land (1970), Peterson & Chalif (1973), Howell & Webb (1995), National Geographic Society (1996), and Edwards (1998). To determine population parameters (Chapter 4.5) the mark-recapture method was applied using individually numbered aluminum bird bands. The following morphometrics of each individual were measured: body mass (with 10.0 g, 30.0 g, 100 g, and 1000 g Pesola spring balances); bill length from tip to proximal end of operculum, bill width and height at operculum, wing length from carpal joint to tip (flattened), length of inner and outermost rectrix from tip to calamus, total length, and tarsus (Figure 6). All morphometrics were measured with a digital caliper (Mitutoyo) to the nearest 0.1 mm and plumage morphometrics to the nearest 1 mm. Body mass was taken from individuals below 30.0 g to the nearest 0.25 g except for Trochilidae (0.1 g), and all other individuals to the nearest 1 g.

Table 2: Dates of standardized mist netting in the cloud forest of Chelemhá in 2001 and 2002. Each date represents a sample of 68 net hours (nh, i.e. hours opened per 12 m net) within the study plot. Net tracks outside the study plot (12 km west of the study plot in Chicacnab) are indicated by *. The dates are distributed over the dry and rainy seasons and over all habitats, see text for further explanation. ^{X} indicates roughly the beginning of the rainy season in May 2002; the first dates in May 2002 belong to the dry season. ^{S} additional net line in the lower parts of the study plot, not included in analyses.

Year:	2001					2002					
Season:	Wet					Dry			Wet		
Month:	June	July	August	September	December	March	April	May		June	July
Day:	05*	15	10	03^{S}	16	16	12	08		06	05
	06*	17	11	05	17	17	13	09		07	06
	07*	18	12		21	18	14	10		08	07
	09*		13		23	20	14	11		09	08
	11*		14				16	12		10	09
	28		16				16	15^{X}		11	10
	30		22				17	16		12	11
			23				17	17		13	12
			25				19	19		14	13
			26				20			15	14
			27				21			16	15
										17	16
										18	17
											20
Days per month:	7	3	11	2	4	4	11	5	4	13	14
Days per season:	23 days (1564 nh)				24 days (1632 nh)				31 days (2108 nh)		
Total:	78 days (5304 nh)										

The fat and muscle stages were determined using a scale between zero (no fat and low muscle) and four (high fat and muscle). The fat and muscle stages were obtained from the belly by blowing the plumage aside. Fat is visible yellow-orange at the distal and proximal end of the sternum. The muscle stages were distinguished by the muscles shape and the visibility of the sternum. Finally, the molt stages of primaries, secondaries, rectrices, and abdominal plumage were recorded. Time and exact location (12 m mist net) of each capture were noted.

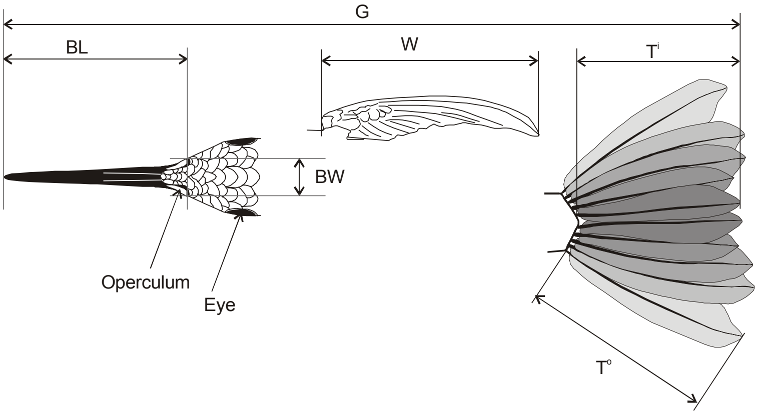

Figure 6: Morphometrics as taken from captured individuals in the cloud forest of Chelemhá. BL: bill length, BW: bill width at operculum, BH at operculum, T^{i}: inner rectrix, T^{o}: outermost rectrix, W: wing (flattened), G: total length. For further explanations see text.

4.4.2 Transect census

After a field learning period of six months in 2001, and by tape recordings provided by the Cornell Laboratory of Sounds, the resident birds were recorded using the male calls and songs (with exceptions, see below). Transects of 150 m were established, 11 in natural forest and nine in young secondary forest; the area covered by one transect is $A = 2rl + \pi r^2$, with r: radius, l: transect length. A maximum of 450 m of transects was conducted per day between the beginning of dawn and 09:00 h. Each transect was visited three times at constant time intervals. The first observations started in late March 2002 and the last were in July 2002 (main breeding season). The observer followed the transect slowly (each 150 m within 30 minutes and backwards another 30 minutes) and recorded each song, call, and sighting. The songs indicate male territoriality (with exceptions, e.g., female Resplendent Quetzal *Pharomachrus mocinno* also call, or Black-Throated Jay *Cyanolyca pumilo* forms breeding groups). The distance of each individual to the transect census point and the vertical stratification (< 7 m, 7 – 20 m, > 20 m) was estimated and mapped.

The area covered by transect census techniques varies with species. Given that the standardized transect census is valid, then per 100 m transect at least 100 m to each side of the path is covered. That indicates an observed area of 2 ha per 100 m of conducted transect. For the 100 m recording distance exceptions are also made. Yellow-Throated Brushfinsh *Atlapetes gutteralis* and Chestnut-Capped Brushfinsh *Buarremon brunneinucha* have an estimated maximum distance of audible sounds of 40 m. Species estimates and densities were corrected with a corresponding factor. The 100 m distance is appropriate for most species, as Terborgh *et al*. (1990) and Thiollay (1994b) also found. Nevertheless, all individuals will never be recorded since they might be hiding or not displaying when the assessment is conducted.

4.4.3 Further recording of birds and behavior

All bird records in the study plot were documented whenever possible and behavior, locations, and numbers were recorded. This method was applied to add rare and vagrant species which were not recorded by standardized methods.

Blue-throated Motmot *Asphata gularis* and Hairy Woodpecker *Picoides villosus* were individually banded with celluloid color leg bands in 2002. The individual spatial and diurnal patterns were observed and (e.g.) individual feeding behavior and territoriality was determined if possible. Unfortunately, the banded individuals were not subsequently observed. Presumably all individuals removed the colored leg band within a short time.

4.5 Statistics and calculation methods

All statistical tests were conducted with Microsoft Excel 2000 and Statsoft Statistica 99. Population and diversity indices were calculated with EstimateS 6.0 (Colwell 2000) and Rarefaction 3.0 (Krebs 1999). The abundance model parameters are calculated with Lognorm and Logseries (Krebs 1999).

All levels of significance are set to $p = 0.05$, unless otherwise indicated.

Because ecological terms are often used in wrong or various contexts (*cf.* Magurran 1988, Rosenzweig 1995, Vanclay 1998, Krebs 1999) a brief summary is given on the terms applied here:

- Species richness simplified refers to the number of species counted. Rosenzweig claims that this term should no longer be used (1995, p. 201). He prefers the term species diversity. Nevertheless, the term species richness is still commonly used. Here it is used in terms of unweighted species numbers.
- Diversity or biological diversity is often used in biological literature in the same way as heterogeneity, i.e. a combination of species richness and evenness (Krebs 1999). Diversity is the weighted species number based on the proportion of abundance.
- The term "biodiversity" was first introduced into biology by Wilson (1988), but is not used here due to unclear definitions and diverse applications and meanings. The Convention on Biological Diversity (CBD; Rio de Janeiro 1992) shows in my opinion the best application for this term. The term "biodiversity" should be avoided concerning diversity *sensu stricto* or in ecology because it is misleading when working with different disciplines and in interdisciplinary research teams.
- Indices of evenness are used to compare two or more samples exclusively or predominantly based on abundance without considering species numbers.
- Similarity here is used in terms of comparison of species composition between two or more samples.
- Species abundance models describe the distribution of abundances and should be used before measuring or estimating any index of diversity to understand the general pattern of the community under consideration (Magurran 1988).
- α-diversity (alpha) is the punctual diversity, here (e.g.) a net line.
- β-diversity (beta) refers to between-habitat or between-sample diversity (species turnover), here all samples within one habitat type or the complete study plot.

4.5.1 Analysis of vegetation structure

The vegetation structure is an important factor determining bird abundance. Selected bird species are correlated with vegetation structure parameters. Selection of species is made where individuals number was at least 10. Additionally, the vegetation structure was analyzed with GIS (see below) and imaged.

4.5.2 Diversity and population indices and estimators

Diversity is usually examined in relation to four main population models. These are the log-normal distribution, geometric series, the logarithmic series and the broken-stick model. All four models have a characteristic shape in a rank/abundance plot (*cf.* Figure 2.4 in Magurran 1988, p. 14). If a community is related to one of the models it is possible to state if the community is impacted (geometric series or log series) or near to optimal conditions if related to log-normal or broken-stick (*cf.* Magurran 1988). The null hypothesis in each case is: the distributions in the population model concerned of observed and expected frequencies are different (p = 0.05). Conclusion: significant differences reject the population model in question. Geometric series patterns are often found in species-poor and/or harsh environmental conditions (Whittaker 1965, 1970, 1972) and are not applicable here ($p <$ 0.01).

Studies involving abundance, species richness, and diversity frequently apply a range of diversity indices and statistical tests (Magurran 1988, Brown 1995, Gaston 1996, Rosenzweig 1995, Cox & Moore 2000, Gaston & Blackburn 2000, and others). Besides diversity estimators and indices, here additionally population size and statistical tests were applied to show differences and similarities between the habitats (natural forest versus young secondary forest) in the study plot in Chelemhá.

The capture data were analyzed in different ways: (i) net line as punctual diversity per temporal repetition (α-diversity), (ii) spatial replicate per habitat as regional diversity (β-diversity), (iii) for understory birds without any input from mid or overstory, and (iv) for the whole study plot.

The observed species number (S_{obs}) is the number of species observed in either habitat or sample. ACE (Abundance-based Coverage Estimator of species richness, S_{ACE}; Colwell 2000) and ICE (Incidents-based Coverage Estimator of species richness, S_{ICE}; Colwell 2000), are relatively new estimators of species richness. Jackknife S_{Jack} and Bootstrap S_{Boot} are two often and commonly used estimators with the same purpose, but which sometimes overestimate numbers (Colwell & Coddington 1994, Colwell 2000). Rarefaction is a method of adapting samples with different sample amplitude for comparison (Krebs 1999).

S_{ACE} is based on the fact that $S_{obs} = S_{rare} + S_{abund}$, with S_{rare} being the number of rare species with 10 or less individuals for all pooled samples and S_{abund} the number of common species with 10 or more individuals for pooled samples.

$$S_{ACE} = S_{abund} + \frac{S_{rare}}{C_{ACE}} + \frac{F_i}{C_{ACE}} \cdot \gamma^2_{ACE} \tag{4.1}$$

with $C_{ACE} = \frac{1 - F_i}{N_{rare}}$, the sample coverage estimate based on the numbers of singletons F_i,

rare species $N_{rare} = \sum_{i=1}^{10} iF_i$, and $\gamma^2_{ACE} = \max\left\{\left(\frac{S_{rare}}{C_{ACE}} \cdot \frac{\sum_{i=1}^{10} i(i-1)F_i}{N_{rare} \cdot (N_{rare} - 1)}\right) - 1.0\right\}$, the estimation of coefficient variation.

Jackknife is based on the observed frequency of rare species in the community. From Heltshe & Forrester (1983), the Jackknife estimate of the number of species is

$$S_{Jack} = S_{obs} + \left(\frac{qs-1}{qs} \right) k \tag{4. 2}$$

with S_{obs} being the total number of observed species, qs the total number of quadrates samples, and k the number of unique species.

Related to the Jackknife estimator, Bootstrap is an alternative for communities with large samples:

$$S_{Boot} = S_{obs} + \sum (1 - p_i)^n \tag{4. 3}$$

with p_i the proportion of the n bootstrap quadrats that have species i present.

The decision which index is used is explained and discussed in Chapter 6.1.

4.5.3 Comparison of habitats, similarity

To compare two or more different areas by diversity, several diversity indices may apply. Here Sørensen[1], Sørensen-Quantitative, and Morisita-Horn (C_{mh}) were calculated. Each index has its intrinsic advantages and disadvantages. Magurran (1988) explains the characteristics of the different indices. Here they are used to compare diversity of natural and young secondary habitats.

Similarity coefficients like the Sørensen (C_s) are widely used, and after Magurran (1988) the following formula was used:

$$\text{Sørensen } C_s = \frac{2j}{Sa + Sb} \tag{4.4}$$

with j being the number of species found at both sites, Sa (Sb) the number of species at site A (B respectively).

The Sørensen-Quantitative index (C_n) takes the abundance of the species concerned into account (Magurran 1988):

$$\text{Sørensen-Quantitative } C_n = \frac{2 \cdot jN}{aN + bN} \tag{4.5}$$

with aN (bN) the total number of individuals at site A (B) and jN the sum of the lower two abundances recorded for species found at both sites.

The only index not influenced strongly by species richness and sample size is the Morisita-Horn index (Wolda 1981).

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[1] The correct spelling is Sørensen after Thorvald Sørensen (1948). There are various spellings in the extensive literature on diversity: Sörensen, Sörenson, Sørenson, Sorenson, Soerensen, and so on in any combination.

$$\text{Morisita-Horn } C_{mh} = \frac{2 \cdot \sum (an_i \cdot bn_i)}{(d_a + d_b) \cdot aN \cdot bN} \tag{4.6}$$

with aN (bN) being the number of individuals at site A (B), an_i (bn_i) the number of individuals of the i-th species in A (B respectively), and $d_a = \Sigma an_i^2 / aN^2$ and $d_b = \Sigma bn_i^2 / bN^2$.

Morisita-Horn, Sørensen and Sørensen-Quantitative were calculated using EstimateS 6.0 (Colwell 2000).

Additionally there are several statistical tests to compare different habitats by (e.g.) species numbers (Sachs 1993, Köhler *et al.* 1993). The nonparametric Mann-Whitney U-test was used to compare two lists, e.g., individual composition in natural forest and young secondary forest.

4.5.4 Evenness

Evenness E (sometimes J') can be taken as the ratio of observed diversity to maximum diversity (Pielou 1969, Magurran 1988).

$$\text{Evenness } E = \frac{H'}{\ln S_{obs}}$$

with H' being the Shannon-Wiener[2] index [$H' = \Sigma(p_i)(\log_2 p_i)$ with p_i the proportion of the total sample belonging to the i-th species], S_{obs} the observed species number. If the ratio E is zero the abundances are completely different and if E is 1.0 the abundances of species equal each other.

4.5.5 Further population parameters

Finally the bird community and subsets of it (feeding guild, specialization, and habitat preferences) were described by several further parameters: abundance, dominance (D_i) and recapture rate (R^t).

4.5.5.1 Dominance

The dominance D_i (common, uncommon, etc.; for definition see Table 3) is defined here as

$$D_i = \frac{n_i}{N} \tag{4.7}$$

with n_i the number of individuals of the i-th species, and $N = \Sigma n_i$. It measures the proportion of the number of individuals of a species to the total number of individuals.

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[2] The spelling "Weaver" is according to Krebs (1999, p. 444) and Schafer (2003) the wrong spelling, instead it is "Wiener".

Table 3: Dominance classes used for the birds at the study plot in the cloud forest in Chelemhá. Status classification follows Howell & Webb (1995).

Class	% class	Status
dominant	> 10 %	common
subdominant	5 - 10 %	fairly common
recendent	1 - 5 %	uncommon
subrecendent	< 1 %	rare

The dominance patterns were first analyzed for the whole bird community and later treated by feeding guild. This emphasizes the distribution of body mass and energy flow (Rosenzweig 1995, Gaston & Blackburn 2000). Finally, dominance was analyzed by guild and habitat (natural versus young secondary forest).

4.5.5.2 Density

Species density (D_y) is a measure used to compare different study plots with each other. It is given in individuals per 100 ha (N_{100}) and an estimation of the expected individuals. Thiollay (1994a, 1994b) used a special treatment for species with flocking behavior and those aggregating in breeding groups. Numbers are given in individuals not pairs, unless otherwise indicated.

Generally the three visits of the transect counts were regarded as sufficient to record territorial displaying by males and/or females during the study period in 2002. According to species, the species numbers per 102 ha obtained were doubled (if only one sex was displaying). The adjustment to 100 ha was ignored due to small differences. Species with lek behavior and breeding groups were adjusted to individuals per 100 ha.

4.5.5.3 Recapture rate

The recapture rate (R^t) of birds is an appropriate method of determining mortality and/or individual turn-over (Mühlenberg 1993, Waltert & Mühlenberg 2001). High recapture rates indicate a high proportion of territorial individuals, long individual presence, and low mortality (Waltert & Mühlenberg 2001).

$$\text{Recapture rate } R^t = \frac{c_i}{r_i} \tag{4.8}$$

with c_i being the first captures of the i-th species and r_i recaptures of the i-th species.

Further aspects of recaptures and recapture rate are discussed in Chapter 6.2.5.

4.5.6 Estimation of population size

The population size was estimated for all species with sufficient recaptures r ($r \geq 1$; Jolly-Seber is dependent on the number of recaptures, Krebs 1999) for the mark-recapture method. The estimation follows the Jolly-Seber estimator (Jolly 1965) for open populations. The estimated population size N_t is (t sample, here: $t = 6$ repetitions):

Estimated population size $N_t = \frac{m_t}{\alpha_t}$ (4.9)

with m_t the estimated size of population at *t-1*, and $\alpha_t = (M_t + 1)/(n_t + 1)$, M_t being the number of marked individuals caught in *t*, n_t the total number of individuals caught in *t*. The estimated population size $\overline{N}_t$ is the mean of all values gathered in the iteration process of the Jolly-Seber estimator: $\overline{N}_t = \frac{\sum N_t}{t}$ (4.10).

For the transect census there were no proper analyses of population size because each transect was repeated only twice. The total number of censuses per transect was three which is not sufficient for the Jolly-Seber estimator of population size (Jolly 1965, Krebs 1999). But the transect census counts were believed to yield all territorial breeding entities and residents when sufficient repetitions were made (see above).

4.5.7 Guild composition

The most abundant guilds are analyzed mainly based on abundance and dominance. For guilds in the Sierra Yalijux the following assumptions were made:

- frugivores: the only bird exclusively feeding on fruits is in Chelemhá Emerald Toucanet Aulacorhynchus *prasinus*. Pigeons were classified mainly as granivores, even if a high percentage feed on fruits. *Asphata gularis* and Blue Mockingbird *Melanotis hypoleucus* were treated in a similar way, but they feed mainly on insects;
- nectarivores: Cinnamon-Bellied Flowerpiercer *Diglossa baritula* and all hummingbirds, even if they are known to perch and feed on small arthropods (Schuchmann 1999);
- carnivorous birds were recorded extremely rarely in the Sierra Yalijux. They were observed high above the canopy or disappearing from the study plot to lower sites;
- omnivores: all species of birds which are known to be dietary generalists or which could not be assigned to one of the above-mentioned groups.

Classification was made using personal observations with additional information from Howell & Webb (1995) and Stiles & Skutch (1989).

There are two approaches to guilds, one considering species numbers and the other considering individuals. The third possibility – a combination of species and individuals – is not useful due to low *N* per guild, habitat, and species.

4.5.8 Understory birds

Waltert (2000) complains that several studies do not sufficiently address issues of the vertical stratification of vegetation and birds' vertical preferences. For instance several canopy species are indifferent if there are three or thirty meters between them and the ground

(Bierregaard & Stouffer 1997). In a special section, the consequences for the assessment of understory bird diversity are examined.

Vertical strata preferences were obtained by transect census techniques and from the literature (Howell & Webb 1995, Stiles & Skutch 1989) and applied to mist netting. Three strata classes were defined (see Chapter 4.4.2 for details).

4.5.9 Body mass

The species, separated into sexes where necessary, were analyzed according to habitat using multivariate analysis (MANOVA). The true understory birds trapped in young secondary forest, i.e. those which were recorded by transect census mainly below 7 m, were grouped in contrast to all birds captured in young secondary forest. Distinguishing between true understory and all captured birds in young secondary forest gives a measure of (i) how indifferent canopy species of natural forest are to height above ground and (ii) if the measured birds "biomass" is comparable. If for instance understory bird body mass is significantly lower in young secondary forest under standardized capturing methods then the habitat may not be suitable for all species and results will decrease body mass per species. This is valid when the feeding guilds in both habitats more or less resemble each other (*cf.* Chapter 5.4.3).

Differences in body mass are an indication of habitat quality and optimal or semi-optimal or even pessimal conditions (*cf.* Winker *et al.* 1995, *cf.* Terborgh *et al.* 1990).

By analyzing body mass, "groups" were classified. A group is either one sex of a given species or a species. Groups were classified in species with high sexual dimorphism and large differences in body mass between males and females. When sexes resembled each other, or were not significantly different in body mass, one species was classified as a group. Immature individuals (characterized by plumage) were generally excluded from body mass analysis.

4.5.10 Morphometrics

After pooling by species and sex, the different habitats were compared with regard to morphometrics. Using a MANOVA (Sachs 1993, Köhler *et al.* 1993), the significant differences between natural forest and young secondary forest concerning morphometrics were calculated.

4.6 Geographic Information System

Distribution of species was imaged using GIS (Geographic Information System, ESRI ArcGIS 8.0). Vegetation structure was linked to the presence of species and the habitat needs of the determined species (compare Kratz & Suhling 1997). The GIS approach was used for Highland Guan *Penelopina nigra*, Mountain Trogon *Trogon mexicanus*, *Pharomachrus mocinno*, Bushy-Crested Jay *Cyanocorax melanocyaneus*, and *Cyanolyca pumilo*.

The area covered by (i) mist netting and (ii) transect censusing was measured using GIS. The detectability of the birds depends on the volume of their voices and for this the area covered by transect censusing depends on the species.

5 Results

5.1 Vegetation structure and birds

Several studies have shown how dependent bird species are on vegetation or vegetation structure (e.g., Slater 1995, Hino 2000). Here, selected species were correlated with one or more of the six vegetation parameters measured. Firstly on a population level then on a community level the dependence of bird species in relation to vegetation parameters is examined.

Selected understory bird species were correlated with vegetation structure (*Diglossa baritula*, *Basileuterus belli*, *Buarremon brunneinucha*, *Henicorhina leucophrys*, *Atlapetes gutteralis*, *Colibri thalassinus*, *Turdus infuscatus*, *Troglodytes musculus*, *Troglodytes rufociliatus*, *Catharus aurantiirostris*, *Asphata gularis*, *Basileuterus rufifrons*, and *Myioborus miniatus*). In particular the understory tree density (UTD), as a measure of the distance from a random locality near a transect census point, was correlated with the frequency of a species. For more precise description and units see Chapter 4.3. The parameters UTH and UTS as well as OTH and OTS are covariables because the taller a tree the larger the diameter (regression of UTH against UTS: $r = 0.93$ $y = 115.40\,x - 0.2197$, $r^2 = 0.872$, $p < 0.01$; OTH against OTS: $r = 0.70$, $y = 38.09\,x - 5.59$, $r^2 = 0.49$, $p < 0.08$). UTS is not used in this context, instead UTH is preferred and OTS and OTH for overstory. The following section describes this significance and which parameters best explain avian abundance. Nevertheless, there are a lot of other factors not yet included which might explain presence and absence or frequency of species. None of the following correlations was significant ($p = 0.05$).

Diglossa baritula is strongly dependent on understory vegetation structure. The higher the understory trees, the less individuals. Understory tree density is the best fitting parameter to explain presence parameters for this species (Table 4).

Basileuterus belli has low affinities to understory vegetation parameters but abundance is negatively correlated to overstory parameters: it is less abundant when overstory trees are taller and canopies broader and lighter (Table 4).

Buarremon brunneinucha abundance is negatively correlated with UTD, i.e. denser vegetation attracts more individuals. While the distribution is explained neither by UTH nor OTD, OTH seems to be a good parameter to explain the frequency. *B. brunneinucha* is most abundant in areas with dense understory and light overstory vegetation. To express this in relative terms, *B. brunneinucha* is more than three times more common in young secondary forest than in natural forest (Table 4).

Atlapetes gutteralis has similar attributes to *B. brunneinucha*, and both are ground-living species. Both species exclusively forage below 2 m above ground. *A. gutteralis* was not found in natural forest and the vegetation structure of young secondary forest does not explain the presence of the species there (no stratification is present and parameters are assigned to the same level as understory in natural forest; Table 4).

The distribution of *Henicorhina leucophrys* does not depend on the measured vegetation parameters. A similar pattern to *B. brunneinucha* is seen concerning overstory: while overstory height is unimportant, overstory density is relatively important (Table 4). *H. leucophrys* needs lighter overstory. Absent stratification as in young secondary forest is a possible explanation because *H. leucophrys* is almost significantly less frequent in young secondary forest than in natural forest (Mann-Whitney U-test: $p = 0.06$).

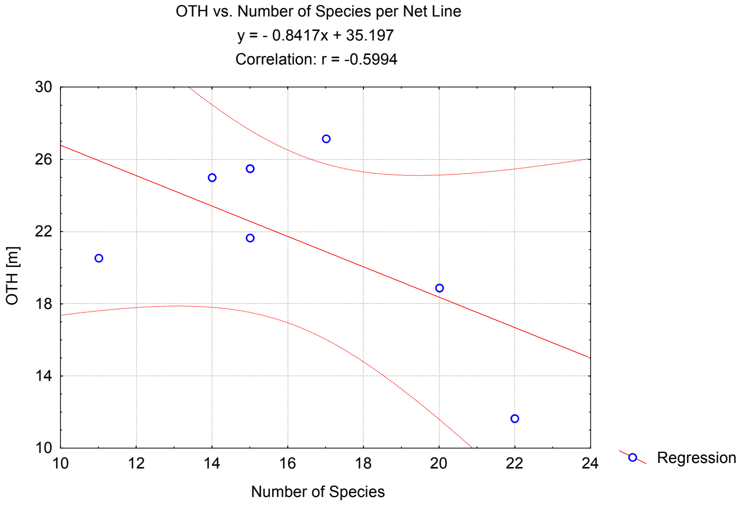


Figure 7: Correlation of tree height with number of species per net line in natural forest.

The two hummingbird species *Colibri thalassinus* and *Hylocharis leucotis* are not dependent on understory vegetation structure. Both species were not captured or observed within forest with more than one layer and canopy above 10 m height (Table 4).

Turdus infuscatus is not present in areas with high or distinctly higher strata but understory structures partly explain individual numbers (Table 4).

Troglodytes musculus, *T. rufociliatus*, *Catharus aurantiirostris*, *Asphata gularis*, and *Myioborus miniatus* had too low numbers to correlate or plot a regression.

Table 4: Multiple regression of number of individuals against vegetation structure parameters in Chelemhá. SD: standard deviation, OTD: overstory tree density, OTH: overstory tree height, UTD: understory tree density, UTH: understory tree height, r^2 corr: corrected r^2.

	ß	SD ß	B	SD B	t(2)	p-level
Diglossa baritula						
r = 0.87	$r^2 = 0.76$	r^2 corr = -				
F(4,1) = 0.81	$p < 0.67149$					
Const.			-11.20	12.48	-0.89	0.53
OTD	1.81	1.41	1.82	1.42	1.287	0.42
OTH	-1.04	1.49	-0.15	0.22	-0.70	0.61
UTD	1.43	1.69	7.38	8.65	0.85	0.55
UTH	0.20	0.59	0.17	0.49	0.34	0.78
Basileuterus belli						
r = 0.95,	$r^2 = 0.90$	r^2 corr = 0.72				
F(4,2) = 5.0521	$p < 0.17$					
Const.			-10.99	22.58	-0.49	0.67
OTD	0.41	0.49	2.57	3.08	0.84	0.49
OTH	-1.39	0.47	-1.26	0.42	-2.97	0.10
UTD	0.63	0.54	19.28	16.42	1.17	0.36
UTH	0.50	0.23	2.35	1.10	2.156	0.16
Hylocharis leucotis						
r = 0.17	$r^2 = 0.03$	r^2 corr = -				
F(2,2) = 0.031	$p < 0.96987$					
Const.			-0.15	25.69	-0.01	0.99
UTD	0.48	1.93	2.97	11.92	0.25	0.82
UTH	0.46	1.93	1.11	4.69	0.25	0.84
Turdus infuscatus						
r = 0.67	$r^2 = 0.45$	r^2 corr = 0.27				
F(2,6) = 2.46	$p < 0.17$					
Const.			0.71	5.48	0.13	0.91
UTD	0.04	0.57	0.18	2.70	0.07	0.95
UTH	0.70	0.57	0.45	0.36	1.24	0.26

	ß	SD ß	B	SD B	t(2)	p-level
Buarremon brunneinucha						
r = 0.97	$r^2 = 0.95$	r^2 corr = 0.85				
F(4,2) = 9.37	$p < 0.099$					
Const.			23.48	15.08	1.56	0.26
OTD	-0.40	0.37	-2.25	2.06	-1.09	0.39
OTH	-0.593	0.35	-0.4791	0.28	-1.69	0.23
UTD	-0.45	0.40	-12.22	10.97	-1.11	0.38
UTH	0.62	0.17	2.59	0.73	3.56	0.07
Henicorhina leucophrys						
r = 0.79	$r^2 = 0.62$	r^2 corr = -				
F(4,1) = 0.41	$p < 0.81$					
Const.			-49.4238	48.34	-1.02	0.49
OTD	1.64	1.31	8.55	6.82	1.25	0.43
OTH	-1.62	1.39	-1.04	0.89	-1.17	0.45
UTD	1.74	1.51	39.34	34.13	1.15	0.45
UTH	-0.01	0.65	-0.045	2.31	-0.02	0.99
Atlapetes gutteralis						
r = 0.70	$r^2 = 0.49$	r^2 corr = 0.24				
F(2,4) = 1.95	$p < 0.26$					
Const.			16.32	6.12	2.67	0.06
UTD	-1.04	0.54	-5.70	2.95	-1.93	0.13
UTH	-0.93	0.54	-1.41	0.82	-1.72	0.16
Colibri thalassinus						
r = 0.31	$r^2 = 0.10$	r^2 corr = -				
F(2,4) = 0.22	$p < 0.81$					
Const.			3.48	6.48	0.54	0.62
UTD	0.22	0.76	0.90	3.14	0.27	0.79
UTH	-0.12	0.76	-0.13	0.87	-0.15	0.89

Assuming that lighter overstory indicates some kind of disturbance (i.e. the overstory is reduced on the micro-scale due to a natural gap), the species number should decline (Intermediate Disturbance Hypothesis of Connell (1978), but see results of Sheil & Burslem (2003)). Number of species per net line (α-diversity) is not significantly correlated with OTD, OTH, UTD, or UTH. But the best explanatory parameter is OTH. In Figure 7 the regression between number of species per natural forest net line and OTH is illustrated (compare data set in Appendix).

While understory tree parameters do not explain species numbers in Chelemhá, overstory parameters contribute in some part to species numbers.

5.2 *Avifauna*

The results presented here only deal with non-migrating birds in the Sierra Yalijux. Neotropical and Nearctic migrants were excluded due to the study period, except for *Wilsonia pusilla* and *Oporornis tolmiei*. The two species identified as migrants (*W. pusilla* and *O. tolmiei*; Howell & Webb 1995) were included because they migrate late in the main breeding season or are present during almost the whole study period.

5.2.1 Observed and expected species

Excluding Neotropical migrants, (all standardized methods) 99 bird species in total were observed in the study plot at Chelemhá. This represents 70.2 % of the expected number of resident birds for Central American highlands above 2000 m (141; Howell & Webb 1995). Seven of the resident birds are listed by Howell & Webb (1995) as having an upper altitudinal limit of 2200 m. The observed species frequency rises to 73.9 % when only species with their upper altitudinal range below 2200 m are included in the expected species list. All species are listed in the Appendix. Three species were not expected and new to the study area (*Dendroica townsendi*, *Volatina jacarina, Carduelis atriceps*).

The study by Eisermann (2000), 12 km west of Chelemhá in Chicacnab, recorded altogether 136 species with 97 residents. The latter represents 68.8 % of the expected species. The author sampled for a complete year and so recorded a high number of migrants, the difference between 136 and 97 (see Appendix). The higher number of observed species in Chicacnab is, although a result of the much larger area covered by the study of approximately 350 ha, in contrast to 102 ha in the Chelemhá plot.

While Howell was not in the Sierra Yalijux (Howell & Webb 1995), he extrapolated the species distribution from other well-known sites, and the deviation will be reasonably high. Nevertheless, the difference between observed and expected species sets is obvious and might be due to a high extinction of species in the Sierra Yalijux (the natural oak-pine cloud forest is reduced to less than 50 % of the original cover). The proportion of migrants and non-residents of 28.7 % in Chicacnab is high and most abundant in secondary vegetation (Eisermann 2000). This could be an indicator for a small carrying capacity of natural forest for breeding birds and migrants; for further discussion see Chapter 6.2. However, fewer species were observed than expected.

5.2.2 Bird community structure

Besides diversity (often used synonymously with heterogeneity), evenness and similarity play an important role in determining community structure and comparing habitats. The following assumptions are made:

- Diversity here is based on the taxon species. Subspecific and generic taxons, even in birds, still remain unresolved and often do not reflect natural relationships (Wolters 1982, Mayr 1999) – the only taxon representing more or less natural entity is the species (compare Wolters 1982, Haffer 1986, Mayr 1999, Renner 2000).
- All species are equally different in function. Sexual dimorphism, body mass, and age stages do not initially influence the analyses.

The purpose of the following sections is to illustrate (i) the overall structure of the bird community, and (ii) the differences between the habitats (natural forest, young secondary forest). Aspects of human impact (iii) and implications for conservation (iv) are discussed in Chapters 6.5 and 6.6.

5.2.2.1 Abundance, dominance, habitat preferences

The commonest species is *Chlorospingus ophthalmicus*, followed by *Lampornis amethystinus* and *Catharus frantzii*. Applying transect census methods, *Ch. ophthalmicus* is followed by *Basileuterus belli* and then by *L. amethystinus*. The most abundant species with *N* > 30 (first captures) are listed in Table 5. Dominance shows the same pattern, which is only obvious considering the definition of dominance (Chapter 4.4.2). The two methods show a clear difference regarding abundance and dominance. The transect census reflects a more precise composition of the breeding bird community because almost all territorially active males, assuming that they are part of a breeding pair, were recorded in a standardized way. In total, 79 species were observed with this method, and in contrast 64 by mist netting. The two methods yielded two different ranks and species sets – as expected (see below).

Table 5: Abundance and dominance of the 10 most frequent birds ($N > 30$) in Chelemhá according to mist netting and transect census (Detections). For further species see Appendix.

	First captures	Recaptures			D_i	Captures		Detections (Ind.)		
Species	Total	Total	NF	YSF		NF	YSF	Total	NF	YSF
Chlorospingus ophthalmicus	148	23	9	14	0.171	57	91	232	212	20
Lampornis amethystinus	126	7	6	1	0.145	76	50	93	70	23
Catharus frantzii	63	35	29	6	0.072	41	22	68	52	16
Lamprolaima rhami	62	12	12	0	0.071	52	10	19	14	5
Diglossa baritula	45	21	0	21	0.052	8	37	11	4	7
Basileuterus belli	39	19	11	8	0.045	24	15	105	67	38
Buarremon brunneinucha	31	7	1	6	0.035	6	25	82	48	34
Henicorhina leucophrys	28	12	10	2	0.032	19	9	57	48	9
Atlapetes gutteralis	23	8	0	8	0.026	2	21	36	15	21
Colibri thalassinus	31	0	0	0	0.035	2	29	12	0	12

NF: natural forest; YSF: young secondary forest; Detections: individuals detected by transect census techniques; Ind.: male individuals (for restrictions and exceptions see Chapter 4); D_i: Dominance of species.

The proportion of singletons, doubletons and unique species to the commoner species is a measure of the completeness of the species inventory. The numbers of species recorded in Chelemhá once or twice is high (Table 11 in Chapter 6) because many species are rare, e.g., dispersing individuals or individuals living at the edge of their suitable ecological range and which are not resident in the study plot (e.g., Begon *et al.* 1996).

A first look at the two different habitats – natural forest and young secondary forest – shows differences in abundance. Figure 8 illustrates the abundance of the 10 commonest species according to mist netting in Chelemhá. *Ch. ophthalmicus* is dominant in both habitats, followed by *L. amethystinus* and *C. frantzii* (see Table 5). Comparing the abundance in both habitats, differences are significant (Wilcoxon test for netted individuals in natural forest and young secondary forest: T = 622.5, Z = 2.639, $p = 0.008$). This means that species are not equally abundant in both habitats.

Few species show preferences for one habitat, i.e. captures or detections are focused on or exclusively in one habitat. All species with five or more captures/detections were assigned to one of the habitats if possible. If 60 % of the individuals of one species were captured or detected in one of the two habitats it was allocated to that habitat ("mainly natural forest"). Exclusively in one habitat are species with more than 95 % captures or detections in one habitat. There were three species mainly recorded (captured and/or detected) in natural forest: *Amazilia cyanocephala*, *Penelopina nigra*, and *Atlapetes gutteralis*. *P. nigra* is even the single species exclusive to natural forest. In young secondary forest there was no exclusively detected species, but three mainly detected species: *Melanotis hypoleucus*, *Buarremon brunneinucha*, and *Cyanolyca pumilo*.

To get an impression of species dominance (for definition and explanation of the terms used here see Chapter 4.5.5.1) regarding guilds, focusing on transect census techniques is the most promising way. The dominance structure in the two habitats is distinctive: there are 56 species in natural forest and 42 in young secondary forest. In natural forest one generalist (*Ch. ophthalmicus*) is the absolutely dominant species (22.2 %), followed by *L. amethystinus* (7.3 %) and *B. belli* (7.0 %). Five species are subdominant and 13 uncommon in natural forest. On the other hand there is no dominant species in the sense of the definition in young secondary forest, but *B. belli* (7.0 %) and *B. brunneinucha* (6.3 %) are subdominant and 31 species are uncommon.

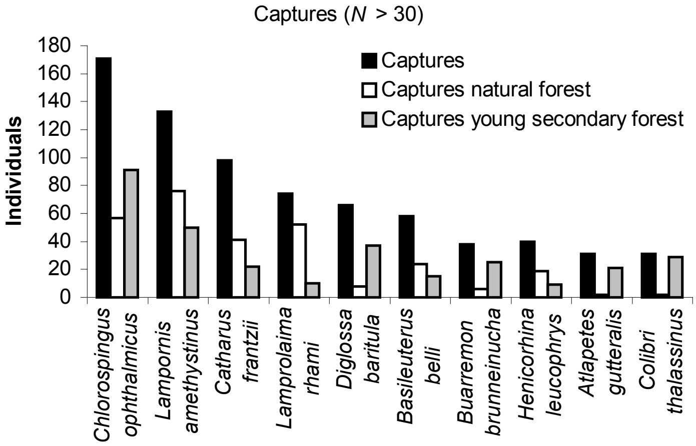


Figure 8: Captures of the 10 most abundant species (*N* > 30) in the study plot at Chelemhá.

5.2.2.2 Guild composition

The guild composition in the study plot in the Sierra Yalijux is dependent on habitat. There are obvious differences when considering (i) species, (ii) individuals, or (iii) sampling techniques (Chapter 4.4.2 and Figure 9). First taking a closer look at species numbers per guild, insectivores are dominant both in natural forest and young secondary forest with approximately 40 %. While frugivores play hardly any role, with less than 3 %, granivores and omnivores are differently abundant in natural forest and young secondary forest. In the latter granivores are more frequent than omnivores but vice versa in natural forest.

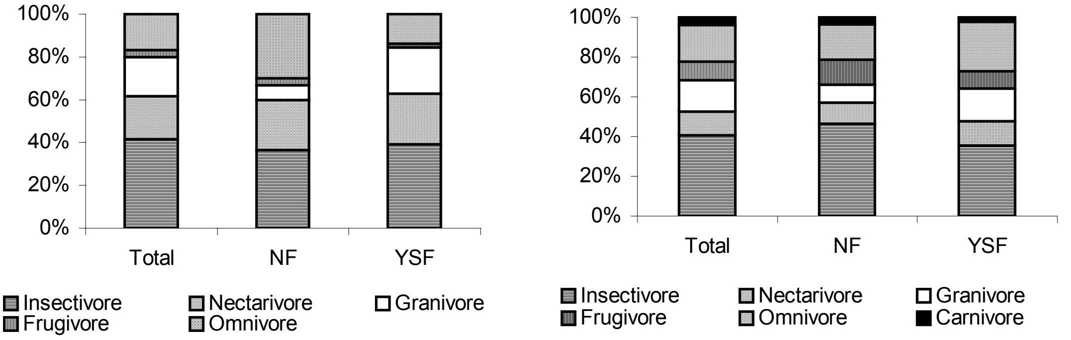
The transect census techniques show a different pattern (Figure 9). Species numbers of all guilds are represented in similar percentages in natural forest and young secondary forest. In natural forest omnivores are more abundant than granivores, in young secondary forest vice versa. Carnivores represent an additional guild, but species and individual numbers are low (Figure 9). Also present are fruit-feeding species in both habitats, with approximately 10 %, and nectarivore individuals are present with also 10 %.

Comparing the two methods for nectar-feeding birds, individual numbers diverge while species numbers are similar to each other.

Further guild composition differences between the habitats are illustrated in Figure 10. All individuals of each guild were grouped independently at species level and related to the total number of individuals in the respective habitat. Carnivores do not play any role, insectivores, nectarivores and frugivores are equally distributed both in natural forest and young secondary forest. Omnivores are dominant in natural forest (45.9 %), but equal in percentage to insect-feeding birds in young secondary forest (29.2 %). Granivores show a different pattern: more frequent in young secondary forest but less frequent in natural forest (19.1 % and 7.6 % respectively).

(a) Mist netting - species

(c) Transect counts - species



(b) Mist netting - individuals

(d) Transect counts - individuals

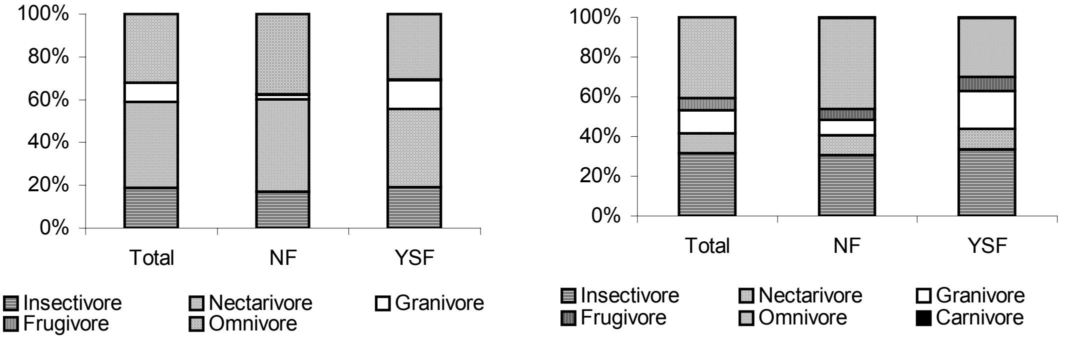


Figure 9: Species numbers and individuals per guild, method, and habitat. (a) Species numbers and (b) individuals per guild by mist netting technique in the study plot (Total), natural forest (NF), and young secondary forest (YSF); (c) species numbers and (d) individuals per guild by transect census techniques in the study plot (Total), natural forest (NF), and young secondary forest (YSF).

Considering individuals the pattern is different: while most species are insectivores most individuals are nectar feeders in both habitats. The percentage of granivorous individuals is higher in young secondary forest at the expense of omnivores compared to natural forest. In both habitats there is a relatively large number of insect-feeding species with at the same time a comparatively low number of individuals, and vice versa for nectar-feeding birds (Figure 9).

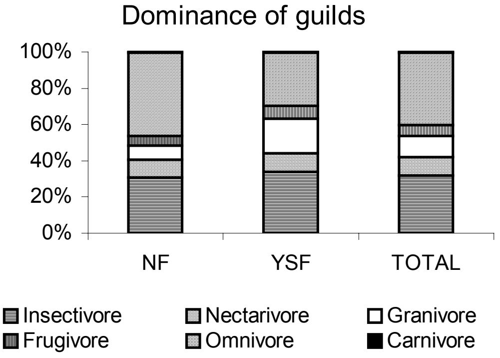


Figure 10: Dominance of guilds in the Chelemhá plot.

5.2.2.3 Species-abundance models

The species-individuals ratio in the total study plot is not distributed like a log series or broken-stick (χ^2 goodness of fit test for both: $p < 0.01$), but with $p = 0.12$ it is distributed log-normally for transect counts. For details on data sets see Appendix and compare Table 6.

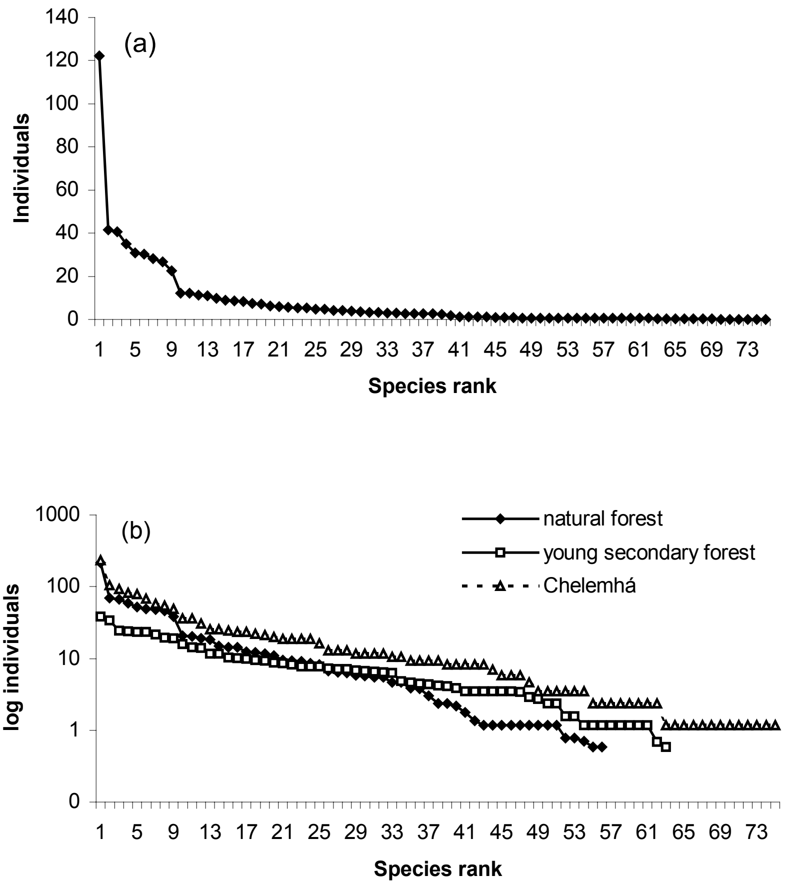


Figure 11: (a) Rank sum plot for detections (individuals per 100 ha) at Chelemhá for 2002. (b) Species rank distribution in the study plot of Chelemhá in relation to habitat using transect census data. All three plots indicate log-norm distribution. For further explanations see text.

5.2.3 Similarity

To compare different habitats or communities – depending on purpose – one might look closer at the differences or similarities of the relevant parameters, here diversity, species richness, abundance, etc. Similarity measures are common methods for distinguishing between entities (Magurran 1988, Rosenzweig 1995, Krebs 1999, Gaston & Blackburn 2000). Based on α- and β-diversity, differences in diversity between habitats were determined for the bird community in the Chelemhá plot.

According to Magurran (1988) and Krebs (1999), the Sørensen and Morisita-Horn indices are more useful than Jaccard or other indices, so here the analyses are based mainly on Sørensen (in Colwell 2000: Sørensen-Inc.), Sørensen-Quantitative (in Colwell 2000: Sørensen-Abd.), and the Morisita-Horn index.

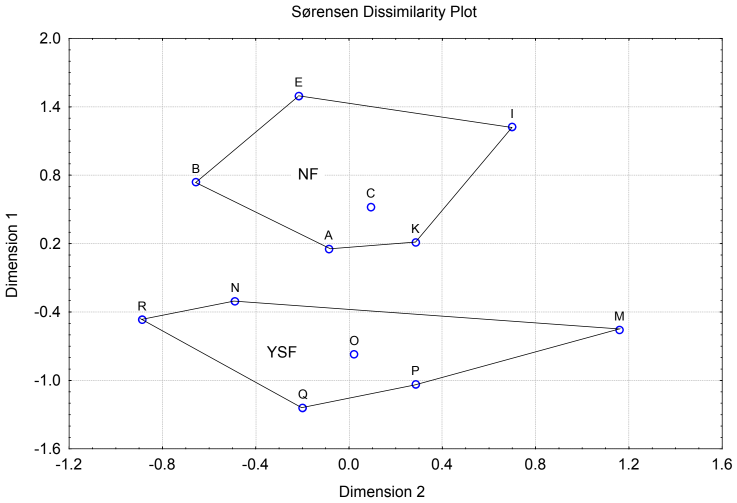


Figure 12: Non-linear multidimensional scaling plot of avifaunal similarity based on Sørensen incidence values. Study sites belonging to the same habitat category are connected by lines. Habitats: NF – natural forest, YSF – young secondary forest. Letters in plot indicate net lines. Note different scaling on axes. For further explanations see text.

For α-diversity, all Sørensen values were arranged in a dissimilarity matrix and a Multi Dimensional Scaling (MDS) was carried out. The results show the β-diversity, i.e. here the diversity changes between the net lines. In Figure 12 the two habitats are grouped and connected by lines to demonstrate the connection. Pair-wise similarity of bird species composition (mean Sørensen ± s.d.) was highest between the six natural forest samples (mist netting), at 0.650 ± 0.11, and intermediate between young secondary forest samples at 0.664 ± 0.34. When ordinating samples using non-linear multidimensional scaling the groups of sites did not show overlap (Figure 12). A one-way MANOVA of the sample scores extracted from the two-dimensional ordination revealed a significant difference between the groups of sites (Rao's $R_{2,9} = 8.27$, $p < 0.01$).

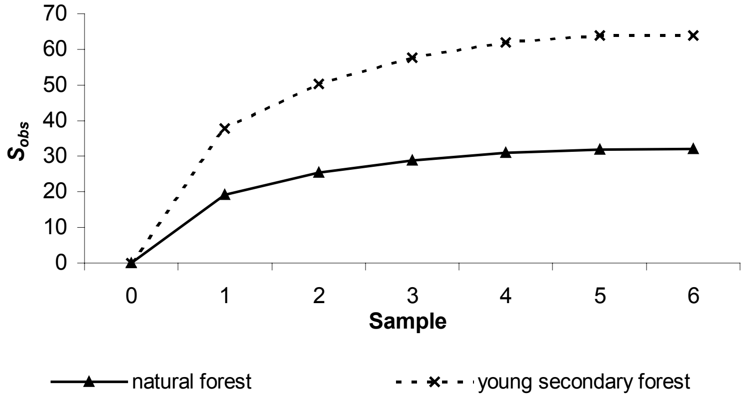
While Sørensen-Quantitative showed clear patterns regarding natural forest and young secondary forest, the Morisita-Horn index gave a conglomerate of non-significant values in the dissimilarity plot ($p > 0.70$).

Considering the twelve net lines, there are two distinct groups readable from the plot in Figure 12, representing natural forest and young secondary forest.

5.2.4 Species richness and diversity

Because of poor definition and terminology, the term “species richness” here is used as unweighted number of species, i.e. individual numbers are not considered in the first step (Magurran 1988, Rosenzweig 1995, Krebs 1999). McIntosh (1967) coined the name for the pure number of species in a sample without weighting. Contrastingly, diversity is referred to as weighted species richness, i.e. species richness combined with abundance. Sometimes this aspect is called heterogeneity. Similarity is focused on the (dis-)similarities between samples of each kind. Last but not least, the term evenness represents the comparison of a hypothetical community with the measured community, to bring out the fact that a community has few common species and many uncommon and rare species (Magurran 1988, Rosenzweig 1995, Krebs 1999).

(a) Observed species



(b) Expected species

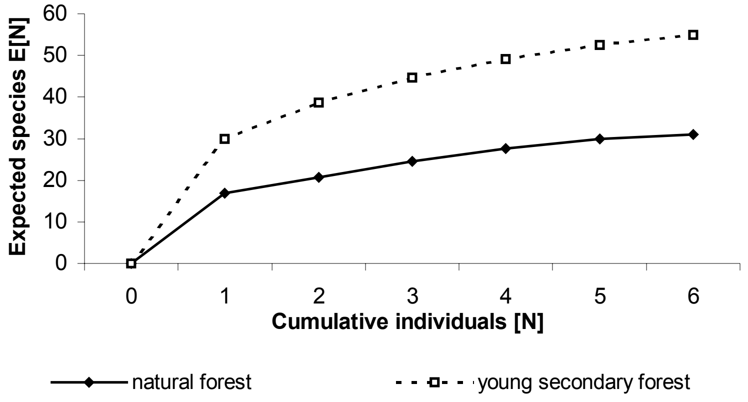


Figure 13: (a) Observed species and (b) standardized samples per individuals (Hulbert Rarefaction) in natural forest and young secondary forest in Chelemhá (calculated following Krebs 1999 and Colwell 2000). Samples are the six repetitions on each net line during study periods in 2001 and 2002. Errors bars were left out for better illustration.

Data analyses is based on both applied methods. The mist net data was arranged in two different ways: (i) the time-based (repetition) analyses of each of the twelve mist nets. This punctual approach measures α-diversity. (ii) The spatial replicates per habitat type, i.e. six of the twelve mist net lines in the habitat were grouped and β-diversity was measured.

Before entering diversity, sample sizes must be standardized and rearranged using the Hulbert-rarefaction method:

Rarefaction standardizes all samples from different communities to a common sample size of the same number of individuals (Sanders 1968). Hulbert (1971) and Simberloff (1972) corrected the rarefaction algorithm of Sanders 1968). All rarefaction curves were calculated with the program Rarefact 3.0 (Krebs 1999).

Rarefaction results are comparable to ACE (Figure 13). Both the estimations for natural forest and young secondary forest coincide with the rarefaction curve. For a transect census with a slightly different sample size (relationship natural forest to young secondary forest area is 11 to 9), the differences from the estimated species numbers (see below) are also similar.

The differences between the two habitats are obvious. The species numbers in young secondary forest are nearly twice as high (33 to 57) as in natural forest, independent of applied method and statistics.

Abundance-based Coverage Estimator and Incidence-based Coverage Estimator (ACE and ICE, Colwell & Coddington 1994) are two relatively new algorithms. They are based on the estimators of Chao and Lee (1992). The problem with the latter was a tendency to overestimation, so Colwell and Coddington (1994) suggested the two new estimators ACE and ICE. Using both, the results from the bird community of Chelemhá are presented and discussed in context with Jackknife and Bootstrap.

Concerning α-diversity, i.e. looking at each single net line's species richness, the clear differences between the two habitats and the contour of several ACE curves is striking. Observed species numbers (S_{obs}) in natural forest lay between 11 and 19. In young secondary forest the species numbers vary between 12 and 30 per net line. The latter index has a higher deviation.

Considering estimated species numbers for young secondary forest, habitat curves show higher variability. ACE even indicates for two net lines (p, m) that saturation of number of species might not be reached. Two net lines show hill-shaped curves (q, r). ACE overestimates samples with small numbers (Matthias Waltert, pers. comm.). Natural forest parameters, both estimated and observed, are relatively closer to each other and are neither hill-shaped nor increasing for the six samples included.

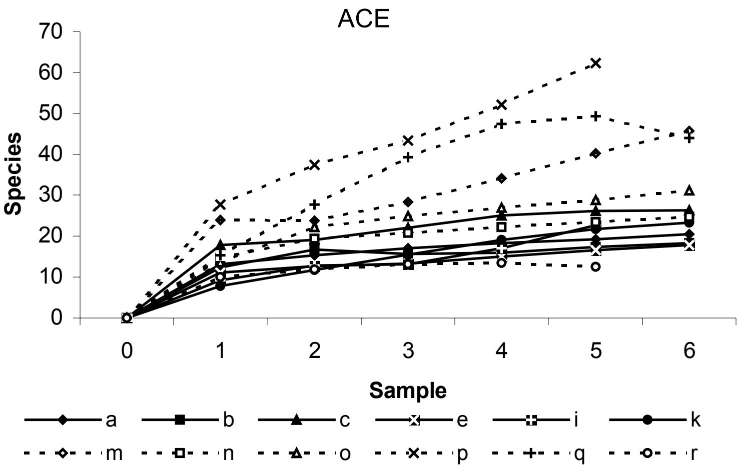


Figure 14: Abundance-based Coverage Estimator (ACE) of species richness (calculated following Colwell 2000) in natural forest and young secondary forest in Chelemhá. Samples are the six repetitions at each net line during 2001 and 2002. Solid lines: natural forest (a to k), dotted lines: young secondary forest (m to r). Standard deviation bars are left out for better illustration.

However it is conspicuous that in natural forest habitats both estimated and observed species are relatively closer to each other than in young secondary forest. The differences between the two habitats are obvious (Figure 14).

In total (all methods, all habitats), 99 bird species were observed in the study plot, 64 by mist netting and 75 by transect census counts. The latter method yielded 1479 individuals in both habitat types of the study plot. The diversity estimates are comparable to mist netting, but transect census has a much lower bias than mist netting (see Chapter 6.1 for discussion). That means that the diversity estimates yield a *per se* higher diversity in young secondary forest than in natural forest. Bootstrap for example in the total Chelemhá plot is 78, in natural forest 50, and in young secondary forest 63. Further species richness estimates are summarized in Table 6 for transect census counts in the Chelemhá plot.

Table 6: Diversity estimates following different estimators for the study plot in Chelemhá calculated with transect census results. NF: natural forest, YSF: young secondary forest, S_{obs}: observed species.

	NF	YSF	Chelemhá
(a) Diversity			
S_{obs}	46.00	58.00	71.12
Singletons	0.09	6.00	10.79
Doubletons	3.00	4.00	6.61
ACE	45.16 (± 1.47)	60.51(± 2.13)	82.11 (± 2.58)
ICE	51.89 (± 2.67)	63.10 (± 1.11)	84.79 (± 1.81)
Jackknife	55.09 (± 5.30)	66.89 (± 4.10)	86.27 (± 5.55)
Bootstrap	50.15 (± 0.00)	62.60 (± 0.00)	78.09 (± 1.54)
(b) Fit for models			
log series	No	No	No
log-norm	Yes	Yes	(Yes)
geometric series	No	No	No
broken-stick	No	No	No

The total number of observed and estimated species in Chelemhá (Figure 15) is 64, independent of estimator (Bootstrap: 67). The differences between the two habitats are manifested here too: in natural forest the estimated species number is 32 (33) and in young secondary forest 57 (60). Mist netting included all or almost all species present in the forest and trappable by mist nets. This is at least true for understory birds (see Chapter 5.2.13).

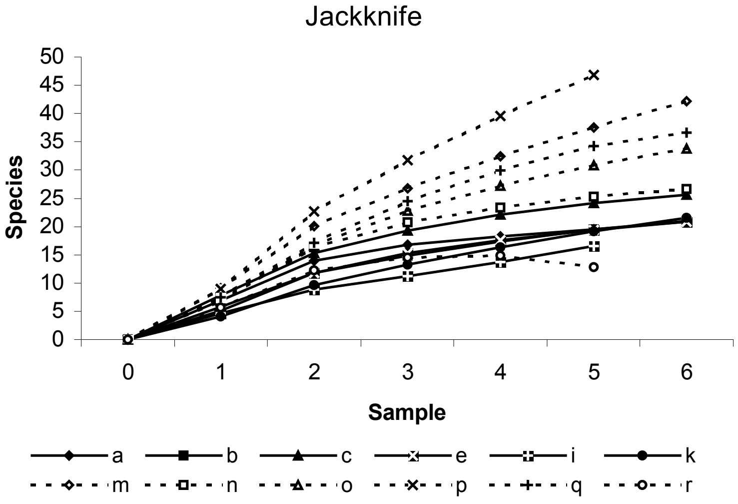


Figure 15: Jackknife in natural forest (solid lines a to k) and young secondary forest (dotted lines m to r) in Chelemhá. Samples are the six repetitions at each net line during 2001 and 2002. Standard deviation bars are left out for better illustration.

By contrast, young secondary forest is seen to be a conglomerate of observed and estimated species numbers with hardly any connection between them. The observed species numbers vary between 12 and 30. The estimated species numbers vary between 12 and 47 (depending on index, here Jackknife).

α-diversity is the same in natural forest at all six net lines, i.e. differences of 11 to 19 species are not significant ($p > 0.01$).

5.2.5 Species-area dependence

Comparing the two different approaches (α- and β-diversity) in analyzing the mist net data, there is a clear visible ecological effect: if area increases, species numbers also increase. The theoretical background is manifested in island biogeography (MacArthur & Wilson 1967) and its diverse alterations, developments, and generalizations. Species numbers increase with increasing area (Figure 16).

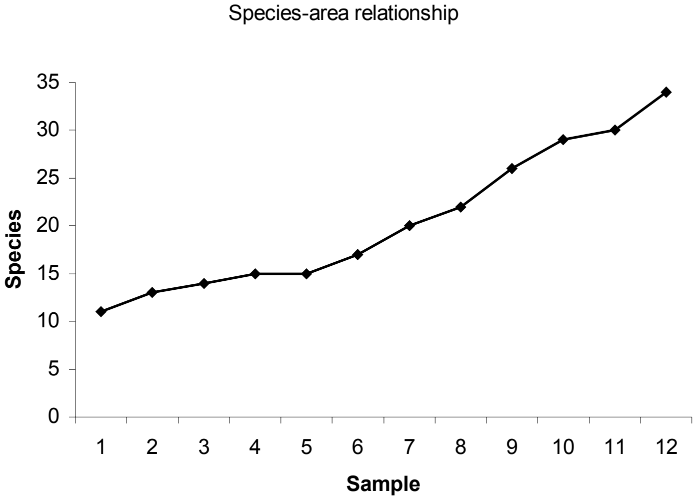


Figure 16: Species-area relationship in the Chelemhá plot. Each net line (sample) represents 16 ha.

5.2.6 Evenness

Communities are composed of species with high abundance plus many rare or uncommon species. Measures of evenness attempt to quantify unequal representation against a hypothetical community in which all species are equally abundant (Krebs 1999). Although a measure of diversity, Shannon's index takes into account the evenness of abundance (Peet 1974), and slightly modified could be used as an evenness measure *E*.

Evenness *E* is 0.620 for the study plot and 0.617 and 0.638 for natural forest and young secondary forest respectively. Evenness is therefore medium, i.e. the abundance distribution of the species is not homogeneous.

5.2.7 Edge effect

The net lines were distributed along a length of 850 m within and outside the natural forest. Several investigations have observed an edge effect concerning species numbers in birds (e.g., Bierregaard & Stouffer 1997), plants and arthropods (e.g., Kapos *et al.* 1997, Didham 1997). Given that species numbers are relatively equal, there is an indication of an edge effect in the Chelemhá plot. Observed and estimated species are higher close to the forest edge and lower away from it. The same pattern is seen with individuals. Closer to the forest edge the individual numbers are higher. From the forest edge outwards into young secondary forest there is, after an initial decrease in species numbers, a sudden increase (Figure 17). However differences are not significant (χ^2 goodness of fit test, $p > 0.05$).

The vague edge effect might be due to the size of the forest fragment (the largest natural forest fragment is approximately 20 km^2, see Chapter 5.1).

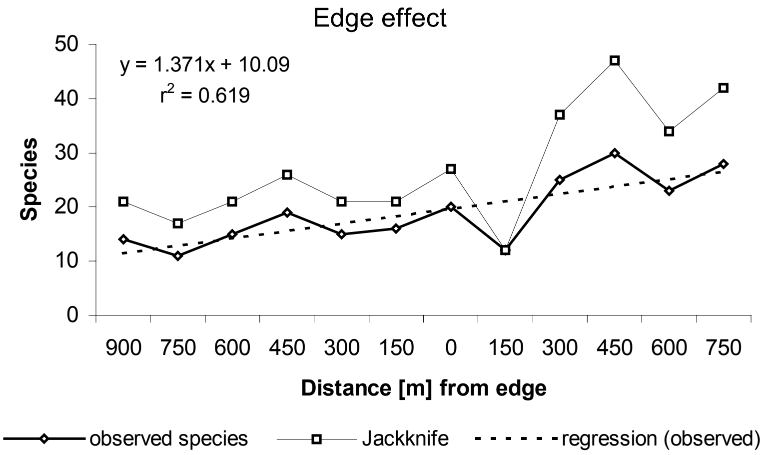


Figure 17: Species numbers distributed according to distance to the forest edge in the Chelemhá plot. On the left are the natural forest, on the right the young secondary forest net lines.

5.2.8 Estimation of population size

The Jolly-Seber algorithm estimates the population size using mark-recapture methods (Jolly 1965). Assuming open populations (Krebs 1999), i.e. allowing for immigration and emigration, Jolly-Seber is superior to the method of Schnabel (1938). The population size was estimated for 14 species in the Sierra Yalijux. The remaining species had no or too few recaptures to apply Jolly-Seber. The estimated population size of (e.g.) *Chlorospingus ophthalmicus* is 191 individuals for the mark-recapture method.

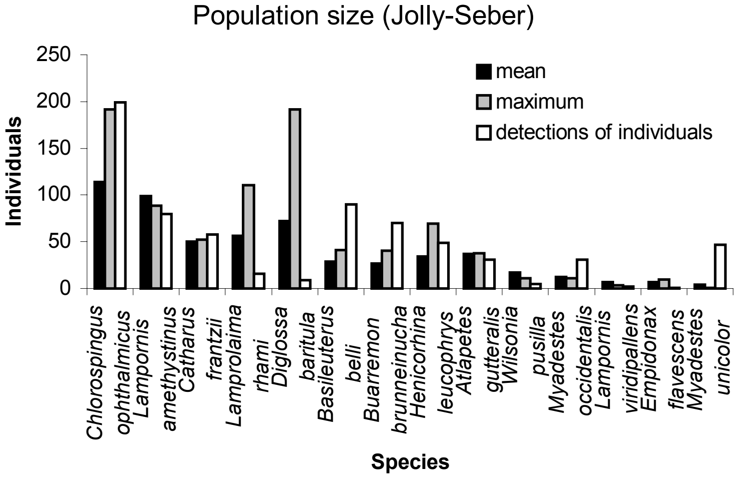


Figure 18: Estimated population size (N_t) from mark-recaptures using the Jolly-Seber method (Jolly 1965) for selected species ($R^t \geq 1$) in the study plot in Chelemhá. Illustrated are mean ($\tilde{N}_t$) and maximum estimated population (N_t) size in the Sierra Yalijux, and estimated number of individuals from transect census techniques (detections of individuals).

Mean and maximum estimated population size for the recaptured birds in Chelemhá equals the transect count estimation (individuals per 100 ha), except for *Ch. ophthalmicus*, *Lamprolaima rhami*, and *Diglossa baritula*. The discrepancies are explained by the different number of recaptures.

5.2.9 Recapture rate

The recapture rate (R^t) is a measure of individual turnover and a possible indicator of mortality in populations (Mühlenberg 1993, Winker *et al*. 1995, Waltert & Mühlenberg 2001, Chapter 6.2.5). Individuals remaining for a long time in a given plot have a higher likelihood of being recaptured, i.e. territorial individuals. It might also indicate compensation for individuals disappearing from the study plot following disturbance. Those individuals are rarely recaptured. Low recapture rate indicates high turnover rate and vice versa.

There are 25 species in Chelemhá with at least one recapture, of which seven had recaptures in both habitats. Twelve species were recaptured exclusively in natural forest and six exclusively in young secondary forest, an indication that the natural forest might be a "better" habitat for birds. Overall, 17 of the 25 recaptured species had at the same time a higher recapture rate in young secondary forest, which indicates the opposite. Even the commonest species (*Ch. ophthalmicus*, *L. amethystinus*, *C. frantzii*) have a three times higher recapture rate in young secondary forest. All three are neither endemic to the Central American highlands, nor feeding specialists nor oak-pine cloud forest specialists. The five endemic species with recaptures in Chelemhá (*Abeillia abeillei*, *D. baritula*, *Empidonax flavescens*, *Asphata gularis*, *Melanotis hypoleucus*) were recaptured with one or two individuals in natural forest and $R^t \leq 0.01$, except for *E. flavescens* with $R^t = 0.20$ in natural forest. Mean R^t is 0.29 and 0.34 in natural forest and young secondary forest respectively.

The recaptures for all 26 species are not significantly different between the two habitats (Wilcoxon test, T = 125.0, Z = 0.714, $p = 0.48$).

Leaving species level and going one step beyond to the individual level, of all 140 recaptures (plus 28 excluded same-day recaptures), 51 were recaptured at the same net line. Except for three, all marked individuals were recaptured in different places within the same habitat. Captures and recaptures were located in natural forest for 68 and in young secondary forest for 69. Of all recaptures, 28 individuals were recaptured twice, one individual of *B. belli* even three times within three months in natural forest at neighboring mist nets (Table 7).

Three individuals changed between habitat types. A female *L. amethystinus* first captured in natural forest on 20 March 2002 was recaptured in young secondary forest on 12 April 2002. One *Ch. ophthalmicus* banded in young secondary forest on 17 July 2001 was recaptured in natural forest on 17 April 2002. One *C. frantzii* first captured in natural forest on 17 March 2002 was recaptured in secondary forest on 17 May 2002.

Table 7: Captures (*c*), recaptures (*r*) and recapture rate (R^t) per habitat in the study plot at Chelemhá. Excluded are all recaptures on the same day.

	c			*r*								Habitat			R^t		
Species	Total	NF	YSF	01	r1	r2	r3	r4	Total	NF	YSF	Both	NF	YSF	Total	NF	YSF
Chlorospingus ophthalmicus	148	57	91	1	12	0	1	0	23	9	14	1	-	-	0.16	0.16	0.15
Lampornis amethystinus	126	76	50	1	2	1	0	0	7	6	1	1	-	-	0.06	0.08	0.02
Catharus frantzii	63	41	22	9	7	3	4	0	35	29	6	1	-	-	0.56	0.71	0.27
Lamprolaima rhami	62	52	10	1	10	0	0	0	12	12	0	0	1	0	0.19	0.23	0.00
Diglossa baritula	45	8	37	7	8	4	0	0	21	0	21	0	0	1	0.47	0.00	0.57
Basileuterus belli	39	24	15	4	5	3	0	1	19	11	8	1	-	-	0.49	0.46	0.53
Buarremon brunneinucha	31	6	25	2	5	1	0	0	7	1	6	1	-	-	0.23	0.17	0.24
Henicorhina leucophrys	28	19	9	6	3	3	1	0	12	10	2	1	-	-	0.43	0.53	0.22
Wilsonia pusilla	25	1	24	1	2	1	0	0	5	0	5	0	0	1	0.20	0.00	0.21
Atlapetes gutteralis	23	2	21	1	2	2	0	0	8	0	8	0	0	1	0.35	0.00	0.38
Myadestes occidentalis	22	1	21	1	2	0	0	0	4	1	3	1	-	-	0.18	1.00	0.14
Lampornis viridipallens	20	16	4	0	1	0	0	0	1	1	0	0	1	0	0.05	0.06	0.00
Empidonax flavescens	18	10	8	1	1	0	0	0	2	2	0	0	1	0	0.11	0.20	0.00
Myadestes unicolor	13	8	5	0	1	0	0	0	1	1	0	0	1	0	0.08	0.13	0.00
Troglodytes musculus	6	0	6	1	1	0	0	0	1	0	1	0	0	1	0.17	-	0.17
Troglodytes ruficiliatus	6	3	3	0	1	0	0	0	1	0	1	0	0	1	0.17	0.00	0.33
Asphata gularis	5	1	4	1	2	0	0	0	2	0	2	0	0	1	0.40	0.00	0.50
Basileuterus rufifrons	3	0	3	0	1	0	0	0	1	0	1	0	0	1	0.33	-	0.33
Oporornis tolmiei	3	0	3	1	1	0	0	0	1	0	1	0	0	1	0.33	-	0.33
Catharus aurantiirostris	2	2	0	0	1	0	0	0	1	1	0	0	1	0	0.50	0.50	-
Melanotis hypoleucus	2	0	2	0	1	0	0	0	1	0	1	0	0	1	0.50	-	0.50
Myioborus miniatus	2	0	2	0	2	0	0	0	2	0	2	0	0	1	1.00	-	1.00
Thryothorus modestus	2	0	2	1	1	0	0	0	2	0	2	0	0	1	1.00	-	1.00
Abeillia abeillei	1	0	1	0	1	0	0	0	1	0	1	0	0	1	1.00	-	1.00
Xiphorhynchus erythropygius	1	1	0	0	1	0	0	0	1	1	0	0	1	0	1.00	1.00	-
Total:	696	328	368	38	60	18	5	1	171	85	86	7	6	12			
Medium Recapture Rate:															0.40	0.29	0.34

01: first capture in 2001, at least one recapture in 2002; r1: one recapture in total, r2: two recaptures in total and so on; Habitat: recapture in both habitats (Both) or exclusively in one habitat; Recapture rate $R^t = r / c$.
NF: natural forest, YSF: young secondary forest.

5.2.10 Transect census

Focusing on the second method applied – transect census – the results are generally comparable to the mist netting results described above. Nevertheless, detailed differences are apparent (see the relevant sections). Because transect counts are not influenced by sampling bias as much as mist netting, results not previously mentioned are presented:

Concerning mist netting, the differences in species numbers and individual composition between natural forest and young secondary forest are significant (see Chapter 5.2.2.1). Applying transect census techniques the differences are not significant (Wilcoxon test: T = 1251.0, Z = 0.919, $p = 0.36$).

Estimation of α-diversity was not applicable due to less temporal repetitions of each transect. Most indices need at least five samples – in this context repetitions – to be calculated properly.

5.2.11 Density of species

Individual density per 100 ha of each species (D_y) is calculated for all species with sufficient data from transect censuses (Table 8). For the calculation of density of individuals per 100 ha see Chapter 4.

The relationship between natural forest and young secondary forest individuals and individual numbers per 100 ha is given in Table 8).

Five endemics with more than 15 individuals (Table 8) show clear preferences in habitat selection. *Notiochelidon pileta* might be overestimated in young secondary forest due to invisibility and inaudible calls in natural forest. *N. pileta* was not recorded in or above natural forest but most likely is abundant there. *Cyanolyca pumilo* and *Troglodytes ruficiliatus* were present nearly twice as much in natural forest as in young secondary forest, while *Penelopina nigra* and *Melanotis hypoleucus* were distributed equally in natural forest and older (!) secondary forest. Further endemics with less than 15 detections were distributed equally (*Strix fulvescens, Lampornis viridipallens*, *Atthis ellioti*, *Trogon mexicanus*) or mainly in young secondary forest (*Turdus rufitorques*, *Cyanocorax melanocyaneus*, *Asphata gularis*).

Species and individual numbers were correlated with vegetation parameters. Multiple regression of the vegetation (OTD, OTH, UTD, UTH; for description of vegetation parameters see Chapter 4) and the individual/species numbers per transect census segment showed no significant correlation between vegetation factors and species numbers per transect section.

The results are also not significant with PCA (Principal Component Analysis) and multiple regression between the parameters mentioned (species numbers [dependent variable] per point against vegetation parameters OTH, OTD, UTD, UTH; with $r = 0.179$, $r^2 = 0.032$, corrected $r^2 = -0.033$, $F_{4,59} = 0.488$, $p < 0.744$, Standard Error: 2.795). This means that species density in the Chelemhá plot is not significantly dependent on the vegetation parameters in the study plot. Nevertheless, the level of significance is almost reached, therefore some relative dependence does exist: the denser any of the four parameters (e.g., denser understory) the more species.

Table 8: Individuals per 100 ha and their proportion in natural forest (% in NF) and young secondary forest (% in YSF) for resident birds in the Chelemhá plot. Data gathered from standardized transect census techniques. * indicates Central American highland endemic (for definition see section 5.2.12, for density calculation see Chapter 4). Species are sorted by total numbers.

Species	NF	YSF	Total	% in NF	% in YSF
Chlorospingus ophthalmicus	213	20	232	0.916	0.084
Basileuterus belli	67	38	105	0.635	0.365
Lampornis amethystinus	70	23	93	0.749	0.251
Buarremon brunneinucha	48	34	82	0.588	0.412
Turdus grayi	59	19	78	0.754	0.246
Catharus frantzii	52	16	68	0.767	0.233
Henicorhina leucophrys	49	9	57	0.851	0.149
Myadestes unicolor	46	9	55	0.840	0.160
Zimmerius vilissimus	39	10	49	0.789	0.211
Myadestes occidentalis	12	24	36	0.340	0.660
Atlapetes gutteralis	15	21	36	0.408	0.592
Thryothorus modestus	20	10	30	0.667	0.333
Mitrephanes phaeocercus	21	5	26	0.812	0.188
Pharomachrus mocinno	18	7	26	0.719	0.281
Quiscalus mexicanus	0	25	25	0.000	1.000
Turdus plebejus	19	4	23	0.812	0.188
*Notiochelidon pileata**	0	23	23	0.000	1.000
*Troglodytes ruficiliatus**	14	8	22	0.652	0.348
Troglodytes musculus	7	14	21	0.316	0.684
Columba fasciata	6	14	20	0.289	0.711
*Cyanolyca pumilo**	12	7	19	0.621	0.379
Turdus infuscatus	12	7	19	0.650	0.350
Lamprolaima rhami	14	4	19	0.762	0.238
*Penelopina nigra**	9	10	19	0.488	0.512
*Melanotis hypoleucus**	9	8	16	0.526	0.474
Total:	941	526	1467	Ø = 0.485	Ø = 0.515

5.2.12 Geographic Information System-based analyses

Analyses by Geographic Information System (GIS) are based on results of the transect census of 2002. *Penelopina nigra*, *Trogon mexicanus*, *Pharomachrus mocinno*, *Cyanocorax melanocyaneus* and *Cyanolyca pumilo* are focused on because they are of increased conservation interest and endemic to the Central American highlands (Chiapas to El Salvador; *Ph. mocinno* to Panamá). GIS-based analyses explain the population distribution in the study plot. By adding more data, like breeding sites and vegetation structure, to distributional patterns, habitat preferences of the species might be determined. The endemic Central American highland species not mentioned (*Strix fulvescens*, *Aspatha gularis*, *Troglodytes rufociliatus*, *Lampornis viridipallens*, *Ergaticus versicolor*, *Notiochelidon pileata*, *Accipiter chionogaster*, *Atthis ellioti*, *Turdus rufitorques*, and *Melanotis hypoleucus*; Stotz *et al.* 1996) have no significance due to the low number of detections and/or captures in this section.

The aim of the GIS-based analysis here is to illustrate and identify habitat preferences and affinities to vegetation structure. All numbers of individuals given are based on estimations and may differ *in vivo* because methods are selective. The most likely number of individuals, and when appropriate the size and extensions of presumed territories, are presented. The individual numbers were determined using the three temporal repetitions of transect census in combination with simultaneously observed individuals. The home range was determined either using the ArcView 3.2 extension “Animal Movement” or by measuring the minimal polygon for appropriate detections ($N \geq 6$). Generally, the population estimations follow the transect counts and yield the same results. Here, minimum and maximum possible estimations of individuals per 100 ha are also given, but in Figs. 19 to 23 the most likely number is given as previously used in analyses of diversity, etc. Further methodological features are explained in Chapter 4.5.5.2.

The five species are of relatively large size (body mass above 30.0 g), which might indicate the higher extinction risk (Cardillo 2003).

5.2.12.1 Highland Guan – *Penelopina nigra*

Forty-two detections were assigned to 13 individuals (Figure 19). A maximal meaningful estimation yielded 20 and a minimal 11 individuals in the Chelemhá plot. Several individuals were observed foraging alongside the territory boundaries and calling or displaying their characteristic descending clapping sounds (individuals 9 and 11; Figure 19).

The estimated minimal home range size of the individuals was between 2.05 and 4.05 ha (individuals 2, 9, 11, and 13 with $N \geq 5$ detections; Figure 19). Mean home range size is 2.97 ha.

5.2.12.2 Mountain Trogon – *Trogon mexicanus*

The closely related species *T. collaris* (Collared Trogon) was recorded for the first time in the Sierra Yalijux and Sierra Caquipec above 2000 m. Two individuals visited the study plot (29 March 2002) before the breeding season, presumably searching for suitable habitats, and were identified by their distinctive under-tail color bands. The remaining 47 records were assigned to *T. mexicanus*.

T. mexicanus is a relatively rare species in the Sierra Yalijux with ten calling individuals in the study plot (Figure 20). The maximum estimated individual number is 11, the minimum seven.

Seven records were made in young secondary forest. All individuals outside natural forest were recorded before the main breeding season, but the distribution is not significant (low *N*). *T. mexicanus* is similarly dependent on natural forest like *Ph. mocinno* (see next section) since it also breeds in excavated breeding cavities. The difference is that *T. mexicanus* does not depend on the characteristic rotten tree stumps but needs old trees (older than about 150 years) and excavated holes.

The estimated minimal home range of the individuals was between 1.19 and 8.94 ha (mean: 4.04 ha, individuals 2, 3, and 5 with $N \geq 6$ detections; Figure 20). The presumed mean range is larger compared with the mean range of *Ph. mocinno* and explains the lower abundance of the first species.

5.2.12.3 Resplendent Quetzal – *Pharomachrus mocinno*

Ph. mocinno was captured once in the study plot but observed several times (60 detections). An assumed 18 males, four females and three immature individuals inhabit the area of the study plot (Figure 21). The maximum possible is 32, the minimal 20 individuals. In the latter case, simultaneously observed individuals were recorded as two, all other values were grouped together. In the first case the entities were grouped as little as possible.

Estimating the individual numbers in the study plot is difficult due to the lek-territory-combination system of *Ph. mocinno*. During pre-breeding, beginning in late January until March, breeding pairs are grouped in lek systems, mostly in exposed trees (own observations, David Unger, pers. comm., Unger 1988). During the lek procedure, and at the latest after maturing, each pair occupies a breeding cavity in suitable tree stumps. Suitable tree stumps are at least 60 cm in diameter and 9 m tall. The holes are excavated mostly one meter below the top of the stump (Figure 5), and all are located between 2.5 and 10 m above ground (Mühlenberg *et al*. 1989). Dead trees with a remaining canopy are not suitable because Quetzals cannot excavate breeding cavities when the stumps are not sufficiently rotten and the wood remains too hard.

Howell & Webb (1995, p. 431) describe how Trogonidae gather sometimes for feeding in trees. The lek system is a more accurate explanation for such a gathering of individuals because it is only seen in *Ph. mocinno* during February and March (own data, Unger 1988). Nevertheless, they gather and feed in fruiting trees for the purpose of mating.

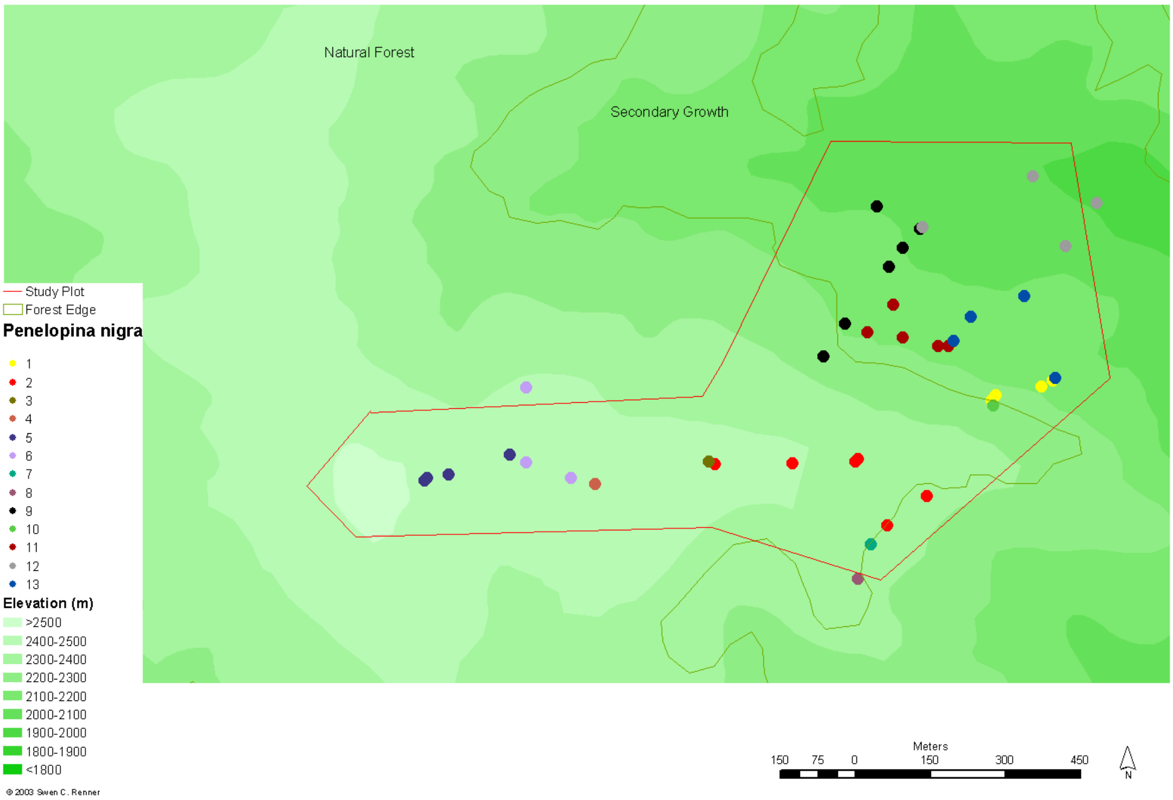
The study plot in the Sierra Yalijux had at least four occupied breeding cavities of *Ph. mocinno* in 2002 (Figure 21). A Total of three different immature individuals was observed in the study plot and breeding success was proved in 2002. Assuming 18 different breeding pairs (each male representing one breeding pair), breeding success was low at 16 %.

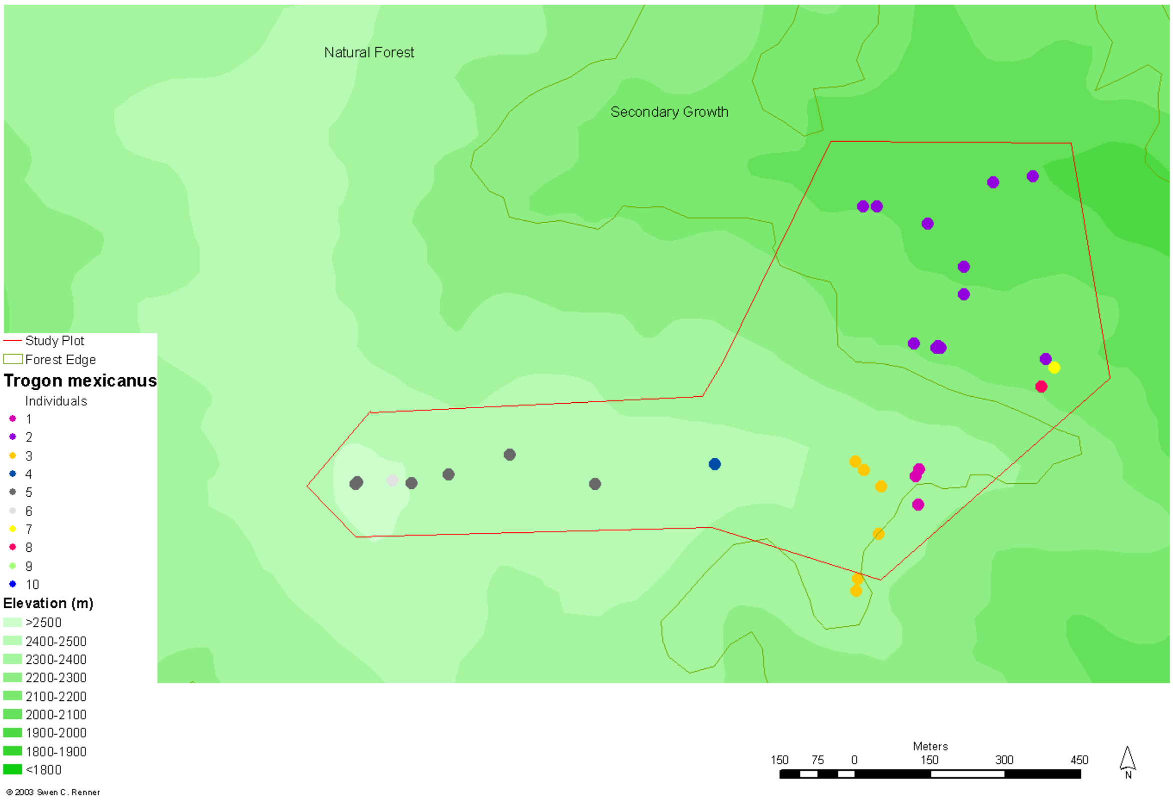
While half of all records are from, or near to young secondary forest, natural forest is essential for the population to survive in the long term. The described breeding holes only are found in old trees which cannot be produced in young secondary forest. While there are still breeding trees for *Ph. mocinno* in young secondary forest, a high percentage of areas are heavily used by humans and the highest and oldest trees do not exceed five years or 10 m. The present breeding holes in young secondary forest might exist for a further 50 years (that is the estimated time for a stump standing upright in *milpa*-system and secondary growth), but thereafter breeding success will be exclusively in natural forest (see discussion Chapter 6.6).

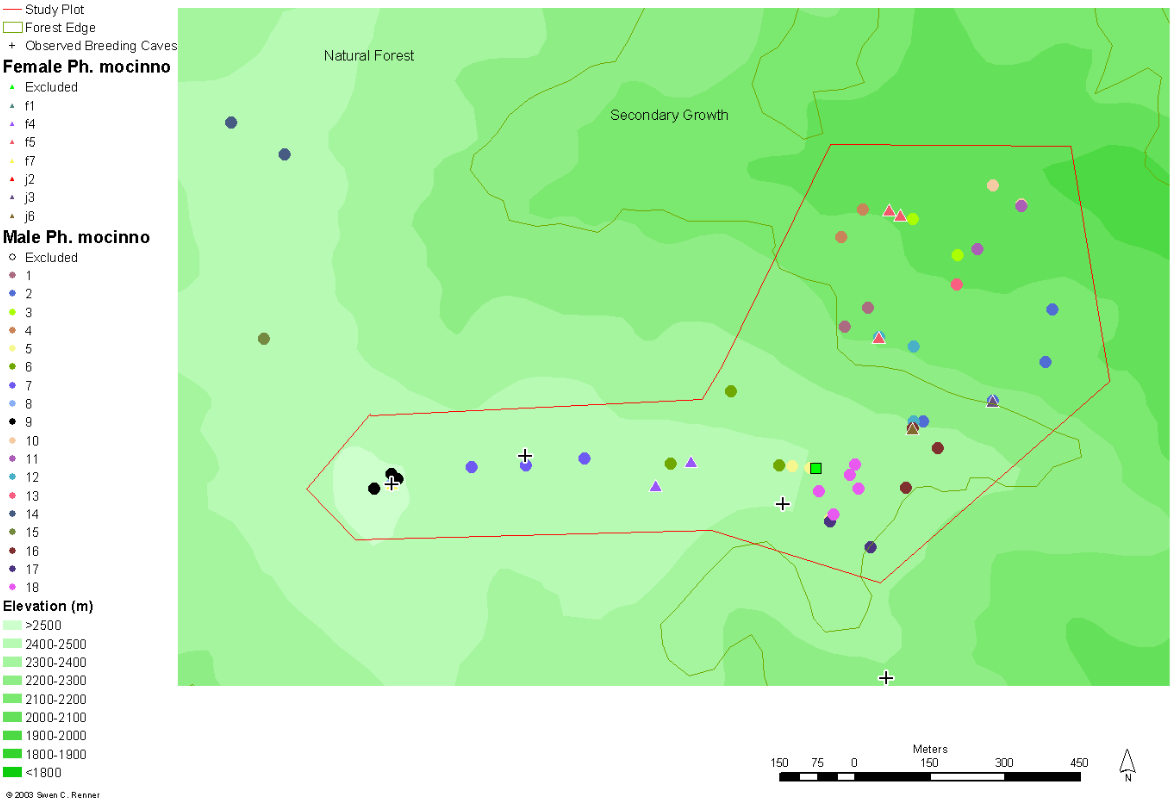
The persistence of *Ph. mocinno* is directly linked to the natural forest as the only source for breeding cavities in the long term. Food is probably not a limiting factor, because several individuals of *Ph. mocinno* were observed feeding in old secondary forest (approximate age of the forest 15 years).

Figure 19 (next page, top): Records of *Penelopina nigra* in the Chelemhá plot. Each color represents one individual. For better illustration records at the same locality were moved 7 m apart. The study plot is indicated approximately by the red line.

Figure 20 (next page, bottom): Records of *Trogon mexicanus* in the Chelemhá plot. Each color represents one individual. For better illustration records at the same locality were moved 7 m apart. The study plot is indicated approximately by the red line.


Natural Forest
Secondary Growth
Study Plot
Forest Edge
Penelopina nigra
1
2
3
4
5
6
7
8
9
10
11
12
13
Elevation (m)
>2500
2400-2500
2300-2400
2200-2300
2100-2200
2000-2100
1900-2000
1800-1900
<1800
© 2003 Swen C. Renner
Meters
150 75 0 150 300 450
N


Natural Forest
Secondary Growth
Study Plot
Forest Edge
Trogon mexicanus
Individuals
1
2
3
4
5
6
7
8
9
10
Elevation (m)
>2500
2400-2500
2300-2400
2200-2300
2100-2200
2000-2100
1900-2000
1800-1900
<1800
© 2003 Swen C. Renner
Meters
150 75 0 150 300 450
N


Study Plot
Forest Edge
Observed Breeding Caves
Female Ph. mocinno
Excluded
f1
f4
f5
f7
j2
j3
j6
Male Ph. mocinno
Excluded
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
Elevation (m)
>2500
2400-2500
2300-2400
2200-2300
2100-2200
2000-2100
1900-2000
1800-1900
<1800
© 2003 Swen C. Renner
Natural Forest
Secondary Growth
Meters
150 75 0 150 300 450
N

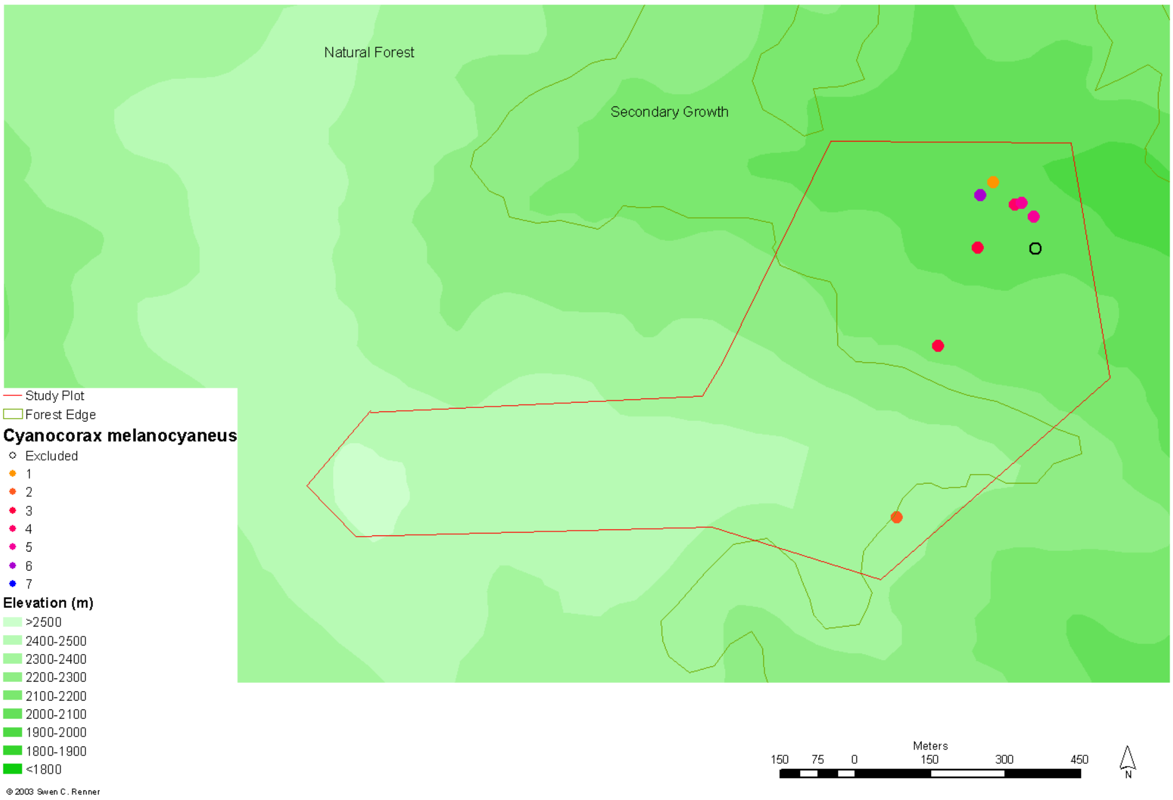
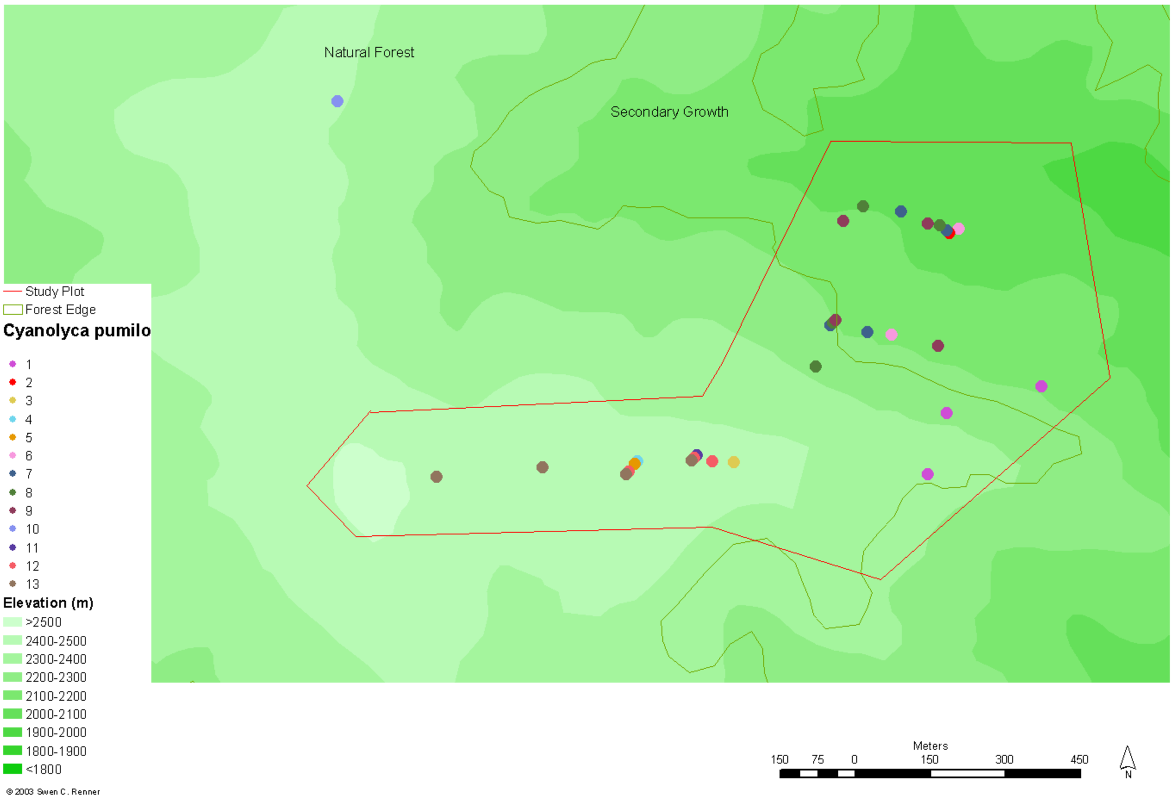

Study Plot
Forest Edge
Cyanocorax melanocyaneus
Excluded
1
2
3
4
5
6
7
Elevation (m)
>2500
2400-2500
2300-2400
2200-2300
2100-2200
2000-2100
1900-2000
1800-1900
<1800
© 2003 Swen C. Renner
Natural Forest
Secondary Growth
Meters
150 75 0 150 300 450
N

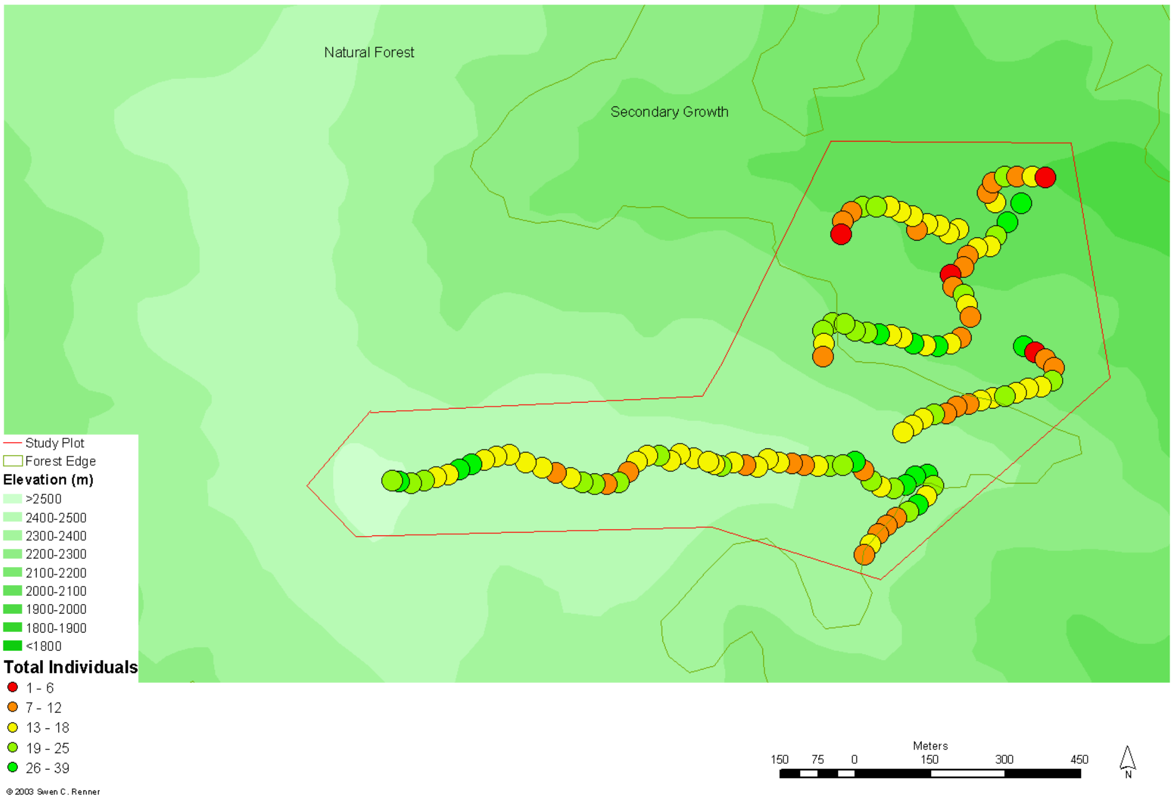
Figure 21 (previous page, top): Records of *Pharomachrus mocinno* in the Chelemhá plot. Each dot represents a male and colored triangles represent female individuals. Illustrated are 18 males, four females (f1, f4, f5, f7), and three immatures (j2, j3, j6), the most likely population of the study plot. For better illustration records at the same locality were moved 7 m apart. The study plot is indicated approximately by the red line.

Figure 22 (previous page, bottom): Records of *Cyanocorax melanocyaneus* in the Chelemhá plot. Each color dot represents one detection, seven individuals were most likely inhabiting the study plot. For better illustration records at the same locality were moved 7 m apart. The study plot is indicated approximately by the red line. Note: *C. melanocyaneus* groups in flocks and forms breeding units greater than two individuals.

Figure 23 (next page, top): Records of *Cyanolyca pumilo* in the Chelemhá plot. Each color dot represents one individual. For better illustration records at the same locality were moved 7 m apart. The study plot is indicated approximately by the red line. Note: *C. pumilo* forms flocks, in Chelemhá presumably one flock of five individuals.

Figure 24 (next page, bottom): Number of individuals of all species projected on the trail system of the Chelemhá plot. The study plot is indicated approximately by the red line. For further explanations see text.


Natural Forest
Secondary Growth
Study Plot
Forest Edge
Cyanolyca pumilo
1
2
3
4
5
6
7
8
9
10
11
12
13
Elevation (m)
>2500
2400-2500
2300-2400
2200-2300
2100-2200
2000-2100
1900-2000
1800-1900
<1800
© 2003 Swen C. Renner
Meters
150 75 0 150 300 450
N


Natural Forest
Secondary Growth
Study Plot
Forest Edge
Elevation (m)
>2500
2400-2500
2300-2400
2200-2300
2100-2200
2000-2100
1900-2000
1800-1900
<1800
Total Individuals
1 - 6
7 - 12
13 - 18
19 - 25
26 - 39
© 2003 Swen C. Renner
Meters
150 75 0 150 300 450
N

Ph. mocinno is a true cloud forest species but immature individuals have been recorded in lowlands (Loiselle *et al.* 1989, Powell & Bjork 1994, 1995). This might be an ancestral relict because many Trogonidae of Central America inhabit tropical lowlands (Howell & Webb 1995) or it might be due to intraspecific competition or foraging behavior due to territories occupied by adults (Winker *et al*. 1995).

The estimated home range size for individuals 7 and 18 was 2.65 and 1.14 ha (Figure 21; $N \geq 6$ detections). All other estimations of home ranges were impossible due to low frequency of detections ($1 \leq N \leq 4$).

5.2.12.4 Bushy-crested Jay – *Cyanocorax melanocyaneus*

Both jay species (see below: *Cyanolyca pumilo*) are believed to forage and breed in colonies or breeding groups (*cf.* Terborgh *et al*. 1990). The breeding group of *C. melanocyaneus* in the Chelemhá plot has most likely seven individuals foraging in young secondary forest (Figure 22).

5.2.12.5 Black-throated Jay – *Cyanolyca pumilo*

It is most likely that all individuals in the plot belong to one single-species flock of five individuals which were moving through the whole study plot in 2002. Four times independently at different sites a flock of five individuals was recorded. The flock occupies the whole study plot alone. Overall, it is also possible, though unlikely, that the study plot contained 13 individuals belonging to three single-species flocks (Figure 23).

Minimum home ranges were not measured because of the unclear territories and flocking behavior.

5.2.12.6 Individual density

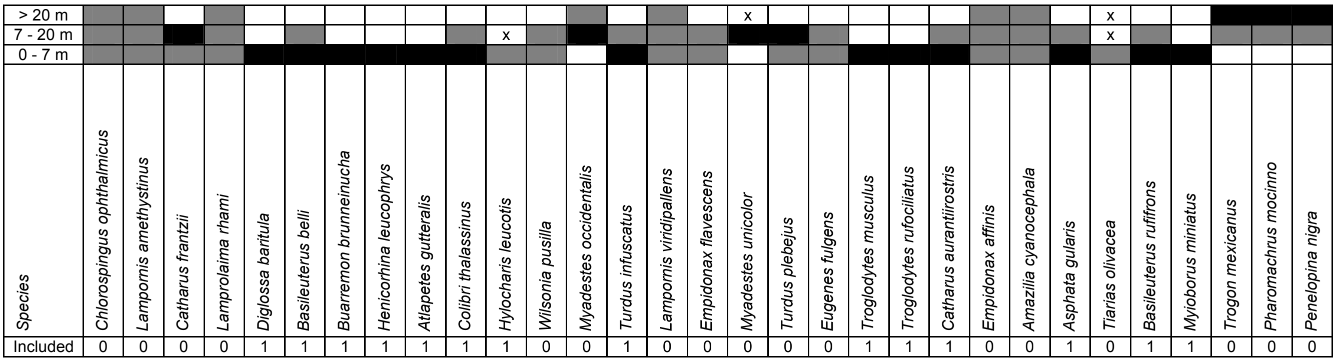
Individual densities (observed number of individuals per point) are illustrated schematically (Figure 24), which means that the distributions are projected onto the trail system. This partly resembles the transect census system, nevertheless trail and transect system show some discrepancies. All species and individuals detected by transect census techniques are summed and projected regardless of date.

Individual numbers per 25 m of transect system show that distribution is heterogeneous (Figure 24), in young secondary forest even more so than in natural forest. Within 25 m differences of the highest and lowest individual class in young secondary forest occur (red: 1 – 6; dark-green: 26 – 39), while in natural forest most trail points have 13 to 18 individuals in total.

There are more individuals near the forest edge (Figure 24). Within secondary vegetation the pattern is heterogeneous compared with natural forest because the secondary vegetation is a highly fragmented mosaic of different age stages.

5.2.13 Understory birds

In this chapter the main analyses are repeated for mist nets in young secondary forest, but without canopy and high strata birds. The point is to show methodological effects and that understory birds in secondary vegetation are impacted by deforestation by removing the influence of canopy species.



> 20 m	▨	▨		▨									▨		▨	
7 - 20 m	▨	▨	■	▨		▨				▨	x	▨	■	▨	▨	▨
0 - 7 m	▨	▨	▨	▨	■	■	■	■	■	■	▨	▨		■	▨	▨
Species	*Chlorospingus ophthalmicus*	*Lampornis amethystinus*	*Catharus frantzii*	*Lamprolaima rhami*	*Diglossa baritula*	*Basileuterus belli*	*Buarremon brunneinucha*	*Henicorhina leucophrys*	*Atlapetes gutteralis*	*Colibri thalassinus*	*Hylocharis leucotis*	*Wilsonia pusilla*	*Myadestes occidentalis*	*Turdus infuscatus*	*Lampornis viridipallens*	*Empidonax flavescens*
Included	0	0	0	0	1	1	1	1	1	1	1	0	0	1	0	0

> 20 m	x						▨	▨		x			■	■	■
7 - 20 m	■	■	▨			▨	▨	▨	▨	x	▨		▨	▨	▨
0 - 7 m		▨	▨	■	■	■	▨	▨	■	▨	■	■			
Species	*Myadestes unicolor*	*Turdus plebejus*	*Eugenes fulgens*	*Troglodytes musculus*	*Troglodytes rufociliatus*	*Catharus aurantiirostris*	*Empidonax affinis*	*Amazilia cyanocephala*	*Aspatha gularis*	*Tiarias olivacea*	*Basileuterus rufifrons*	*Myioborus miniatus*	*Trogon mexicanus*	*Pharomachrus mocinno*	*Penelopina nigra*
Included	0	0	0	1	1	1	0	0	1	0	1	1	0	0	0

Figure 25: Detections of vertical stratification in classes of common species (*N* ≥ 5) in the Sierra Yalijux. Blank squares indicate no record, gray few records, and black high frequency, x indicates no safe records for the species in the relevant vertical stratum. The final (Included) row indicates inclusion in analyses concerning diversity indices, body mass and correlations with vegetation (1: included, 0: excluded). Species are sorted by captures.

Species show preferences by changing abundances depending on strata. In Figure 25 the vertical stratifications of birds with more than 10 captured individuals are classified according to three vertical classes: 0 – 7 m above ground, 7 – 20 m, and > 20 m. The observations were made during transect censuses and incidental observations and afterwards adopted to mist netting data. In a first step only captured individuals with $N \geq 5$ are included (illustrated in Figure 25), then in a second step species with clear understory preferences and captures $N \geq 1$ (*Thryothorus modestus*, *Automolus rubiginosus*, *Melanotis hypoleucus*, *Melozone biarcuatum*, *Sporophila torqueola*, *Zonotrichia capensis*, *Claravis mondetoura*, *Grallaria guatimalensis*).

Figure 26 illustrates the pattern of vertical stratification for all species captured ($N \geq 5$) in the study plot. As expected most species have their main vertical range below 20 m, and most were even recorded below 7 m. The observations of strata preferences were made during transect census counts. After that, analyses of mist netting data were resumed with the exclusion of overstory or canopy species. Bell (1982), Popma *et al.* (1988), Terborgh *et al.* (1990), and Thiollay (1994a) counted most species near the ground with a second peak in the canopy.

For all 14 species recorded mainly below 7 m and not above 20 m in natural forest by transect census counts, the most important analyses for netting data were resumed, i.e. comparison between habitats, similarity and diversity.

The problem in excluding non-understory birds are those species with few sight records and few captures but at the same time with unclear vertical stratification distribution. They are difficult to assign to a specific stratum and several are possibly excluded because of too few records. Where possible, vertical stratification data was assigned from literature (Land 1970, Stiles & Skutch 1989, Howell & Webb 1995). Nevertheless, in Figure 26 species are plotted for natural forest and young secondary forest. There are differences between the habitats, but all estimated and observed species numbers are similar at between 10 and 13 in natural forest, 13 in young secondary forest, and 14 to 15 in the total study plot. Only the shape of the curves (Figure 26) are distinct: young secondary forest has hill-shaped curves while natural forest has more convex shapes.

Estimating diversity for all 22 species with a main vertical range below 7 m with any numbers of captures (Figure 27), the general pattern is slightly different. Considering natural forest species as expected and young secondary forest as observed species the differences are significant (Mann-Whitney U-test, $p < 0.01$).

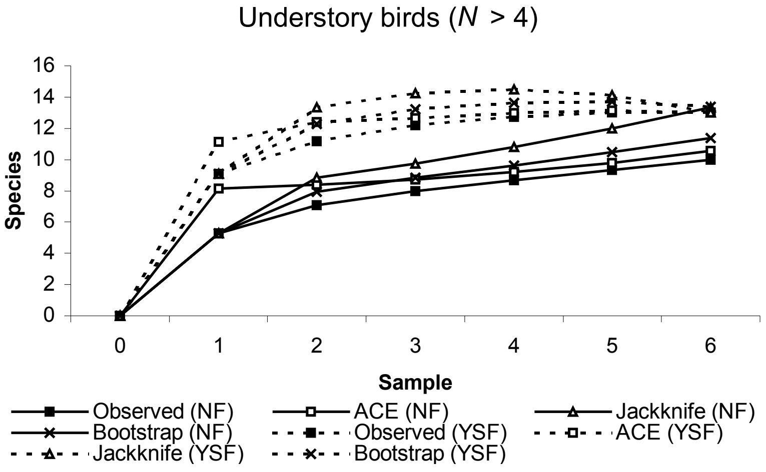


Figure 26: Observed species, ACE, Jackknife, and Bootstrap for understory birds in the Chelemhá plot. Included are all captured species with a main vertical distribution below 7 m and at least five captures ($N \geq 5$). Solid line (NF): natural forest, dotted line (YSF): young secondary forest. See text for further explanations. Error bars are left out for better illustration.

The lower differences in diversity between natural forest and young secondary forest is an indication that young secondary forest is, in this case study, not an equivalent habitat for understory birds because the differences are significant. The reproductive success of the species must be evaluated.

If more species with understory preferences are added and the definition for inclusion into understory bird analyses expanded, a continuum from small differences to maximum differences will result (Figure 32).

The differences are also clear in shape of the Sørensen plot of dissimilarity (Chapter 5.2.3, Figs. 12 and 28). After performing a multidimensional scaling with Sørensen-index, understory birds are seen to be different between natural forest and young secondary forest (Rao's $R_{2,9} = 9.67$, $p < 0.01$). Species richness in itself is less distinct but species composition shows clear differences.

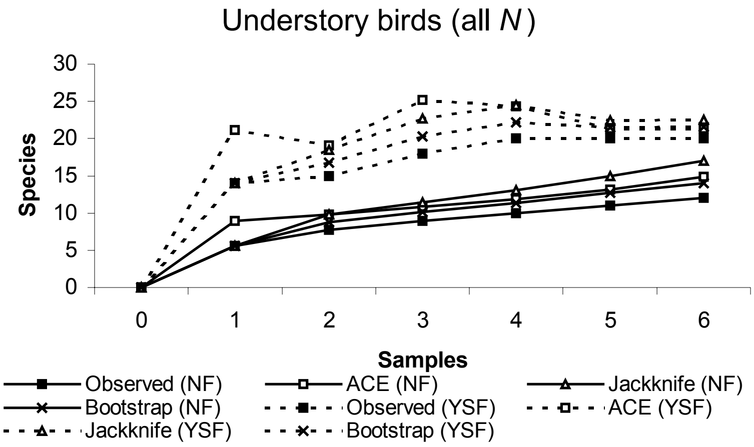


Figure 27: Observed species, ACE, Jackknife, and Bootstrap for understory birds in the Chelemhá plot. Included are all species captured below 7 m ($N \geq 1$). Solid line (NF): natural forest, dotted line (YSF): young secondary forest. See text for further explanations. Error bars are left out for better illustration.

In Figure 28 the two habitats are grouped and connected by lines to demonstrate the connection for understory birds in the Chelemhá plot. Pair-wise similarity of bird species composition (mean Sørensen ± s.d.) was highest between the six natural forest samples (mist netting), amounting to 0.493 ± 0.15, and intermediate between young secondary forest samples, 0.758 ± 0.08. When ordinating samples using non-linear multidimensional scaling the groups of sites did not show overlap (Figure 28). A one-way MANOVA of the sample scores extracted from the two-dimensional ordination revealed a significant difference between the groups of sites (Rao's $R_{2,9} = 9.67$, $p < 0.01$).

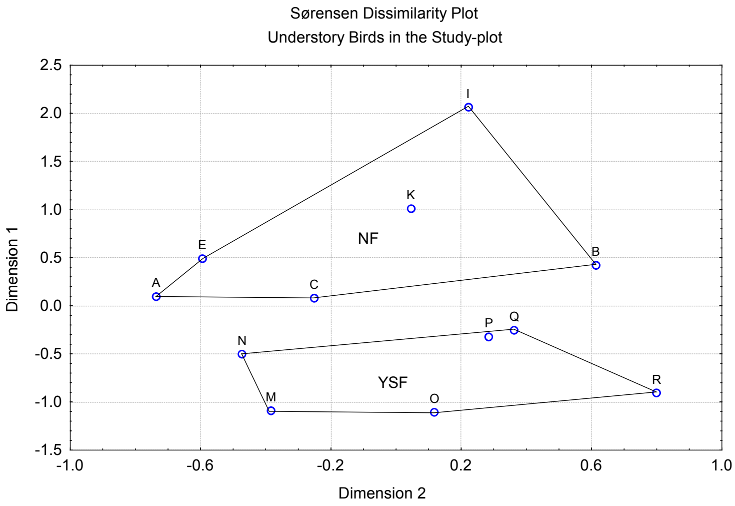


Figure 28: Non-linear multidimensional scaling plot of avifaunal similarity based on Sørensen incidence values for understory birds in the Chelemhá plot. Study sites belonging to the same habitat category are connected by lines. Habitats: NF – natural forest, YSF – young secondary forest. Letters in plot indicate net lines. Note different scaling on axes. For further explanations see text.

However, using the Sørensen-Quantitative and the Morisita-Horn indices in multidimensional scaling does not provide a clear distinction between the two habitat types ($p > 0.05$).

5.3 Body mass

Body mass analyses often indicate differences in habitat quality. Body mass is linked to guild composition because feeding habits will influence the body mass of individuals and more general traits of a species belonging to such a guild. At one site, many carnivores and fruit-feeding birds are larger, at another most nectar-feeding birds are comparably small (Böhning-Gaese 1997, Lafferty & Curis 2002, Cardillo 2003).

In natural forest and young secondary forest there are several distinguishable traits of the communities in the two habitats: the total "biomass" of birds (860 individuals in total included) in the study area (i.e. the mass of all captured individuals; [in brackets: estimated body mass for all individuals detected using transect census techniques in g/100 ha]) is 39 398.0 g [78 031.0 g], distributed over natural forest (16 486.6 g [40 973.4 g]) and young secondary forest (22 911.4 g [37 057.6 g]). Assuming that body mass is a measure of productivity (Terborgh *et al.* 1990), young secondary forest might be less productive regarding birds than natural forest, but see Discussion. The situation is more extreme for exclusively understory birds (section 5.2.13). Only 435.0 g of the total body mass in young secondary forest belongs to "true" understory birds. Expanding the definition of understory birds, the body mass distribution increases to 3279.6 g for all first captures (without recaptures). Nevertheless, this is about a tenth of the total body mass and is seven times less than for all birds in young secondary forest. In transect censuses 7055.4 g/100 ha for all understory birds was measured.

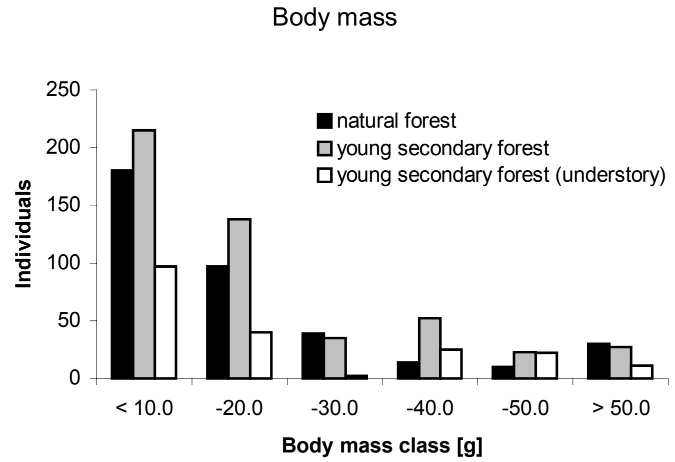


Figure 29: Body mass distribution in the Chelemhá plot in natural forest, young secondary forest and understory birds of young secondary forest (understory).

Thirteen of the 23 groups (a group is either a species or one sex of a species; for *Diglossa baritula*, *Lampornis amethystinus*, *L. viridipallens*, *Lamprolaima rhami*, and *Turdus infuscatus* a sexual separation for analysis is essential due to significant body mass differences between both sexes, see Methods) with at least two individuals in each habitat have a higher mean body mass in young secondary forest. The differences are not significant (MANOVA, variable: habitat, $p = 0.21$, Post-hoc: Newman-Keuls test). However, taking into consideration only understory birds, there are significant differences between the two habitats ($p < 0.01$).

Individual recaptures show that three out of 180 recaptures changed habitat during the study period in 2001 and 2002. Two of the three were first captured in natural forest and one moved into natural forest after being marked in young secondary forest. Unfortunately, *N* is to small to employ any test. Two habitat-switching individuals had a higher body mass in young secondary forest than in natural forest (*Lampornis amethystinus* 5.5 g → 6.5 g, *Catharus frantzii* 26.0 g → 28.3 g). One decreased dramatically in body mass (*Chlorospingus ophthalmicus* 16.5 g → 8.5 g).

Thirty-nine of 107 individuals showed a decrease in body mass at the first recapture, 11 in fat classes and 15 in muscles classes.

Table 9: Mean body mass in g (BM) of captured birds and detected individuals in Chelemhá. N: mist net captures (without recapture), TC: number of individual records from transect census techniques. Missing body mass data was compiled by data from Dunning (1993). NF: natural forest, YSF: young secondary forest, YSF (Understory): body mass of understory birds in young secondary forest. See text for further explanations.

		Body mass							
		Total per species		NF		YSF		YSF (Understory)	
Species	BM	N	TC	N	TC	N	TC	N	TC
Chondrohierax uncinatus	278.0		324.4				324.4		0.0
Ortalis vetula	563.0		1972.6		328.6		1644.0		0.0
Penelopina nigra	890.0		16625.2		8108.5		8516.6		0.0
Dendrortyx leucophrys	350.0		1226.3				1226.3		1226.3
Cyrtonyx ocellatus	200.0		233.6				233.6		233.6
Columba fasciata	342.3		6794.6		1966.0		4828.5		0.0
Claravis mondetoura	73.0	4599.0		2993.0		1606.0		1606.0	
Geotrygon albifacies	304.0	2432.0		608.0		1824.0			
Bolborhynchus lineola	53.6		312.8		250.3		62.6		0.0
Ciccaba virgata	250.0		291.8		291.8				
Strix fulvescens (superspecies with *varia*)	716.5		836.3		418.2		418.1		0.0
Caprimulgus (*vociferus*) *arizonae*	53.0		247.2				247.2		0.0
Cypseloides niger	45.6		159.8				159.8		0.0
Aeronautes saxatalis	32.1		37.5		37.5				
Campylopterus hemileucurus	10.6	328.6		63.6		265.0			
Colibri thalassinus	5.4	5.4	63.1	0.0		5.4	63.1	5.4	63.1
Abeillia abeillei	3.4	130.7	7.8	80.4	3.9	50.3	3.9		0.0
Hylocharis leucotis	3.4	3.4		3.4		0.0		0.0	
Amazilia cyanocephala	5.9	146.3		5.9		140.4			
Lampornis viridipallens	5.6	705.6	13.1	425.6	6.5	280.0	6.5		0.0
Lampornis amethystinus	5.7	176.7	532.3	0.0	398.5	176.7	133.9		0.0
Lamprolaima rhami	6.9	138.0	128.9	110.4	98.2	27.6	30.7		0.0
Eugenes fulgens	7.7	139.1	9.0	77.3		61.8	9.0		0.0
Doricha enicura	3.1	3.1		0.0		3.1			
Tilmatura dupontii	2.2		2.6				2.6		0.0
Atthis ellioti	2.4	12.2	19.9	4.9	11.4	7.3	8.5		0.0
Trogon collaris	64.4		150.3		150.3				
Trogon mexicanus	69.3		647.2		380.7		266.6		0.0
Pharomachrus mocinno	220.0	220.0	5650.3	220.0	4063.9	0.0	1586.4		0.0
Asphata gularis	55.4	55.4	452.8	0.0	75.4	55.4	377.4	55.4	377.4
Aulacorhynchus prasinus	154.5	772.5	1262.7	154.5	841.6	618.0	421.1		0.0
Picoides villosus	35.0	35.0	449.5	35.0	329.6	0.0	119.9		0.0
Colaptes auratus	124.5	18426.0	726.8	7096.5	218.0	11329.5	508.8		0.0
Automolus rubiginosus	47.8	1099.4	446.6	95.6	103.0	1003.8	343.6	1003.8	343.6
Sclerurus mexicanus	25.0		233.5		233.5				
Xiphorhynchus erythropygius	41.1	41.1	95.9	41.1	32.0	0.0	64.0		0.0
Lepidocolaptes affinis	27.5	1705.0	32.1	1430.0	32.1	275.0			
Grallaria guatimalensis	88.3	88.3		0.0		88.3		88.3	
Camptostoma imberbe	13.3	39.9		0.0		39.9			
Zimmerius vilissimus	11.3	11.3	554.1	0.0	437.0	11.3	117.1		0.0
Mitrephanes phaeocercus	8.6		220.9		179.4		41.4		0.0
Cantopus pertinax	27.2		31.8		31.8				
Empidonax affinis	17.0	765.0		136.0		629.0			
Empidonax flavescens	12.2	12.2	14.2	0.0	14.2	12.2			
Vireo plumbeus	20.3	20.3	165.5	0.0	165.5	20.3			
Cyanocorax melanocyaneus	106.0	212.0	866.5	0.0		212.0	866.5		0.0
Cyanolyca pumilo	49.3	1528.3	921.0	98.6	571.5	1429.7	349.4		0.0
Corvus corax	1200.0		1400.8		1400.8				
Tachycineta thalassina	14.2		16.6				16.6		0.0

		Body mass							
		Total per species		NF		YSF		YSF (Understory)	
Species	BM	N	TC	N	TC	N	TC	N	TC
Notiochelidon pileata	12.2		284.8				284.8		0.0
Thryothorus modestus	17.3	34.6	525.1	0.0	350.0	34.6	175.1	34.6	175.1
Troglodytes musculus	11.3	67.8	237.5	0.0	75.0	67.8	162.5	67.8	162.5
Troglodytes rufociliatus	11.3	67.8	250.6	0.0	163.4	67.8	87.2	67.8	87.2
Henicorhina leucophrys	14.5	14.5	829.4	0.0	706.0	14.5	123.4	14.5	123.4
Myadestes occidentalis	36.1	36.1	1306.8	0.0	443.7	36.1	863.1		0.0
Myadestes unicolor	38.6	849.2	2117.8	38.6	1778.9	810.6	338.9		0.0
Catharus aurantiirostris	28.8	57.6	369.8	0.0	184.9	57.6	184.9	57.6	184.9
Catharus frantzii	27.3	54.6	1848.4	0.0	1418.5	54.6	429.9		0.0
Turdus infuscatus	73.4	220.2	1371.1	220.2	891.1	0.0	480.0	0.0	480.0
Turdus plebejus	79.5	1828.5	1856.0	1351.5	1508.0	477.0	348.0		0.0
Turdus grayi	69.0	414.0	5396.8	207.0	4066.9	207.0	1329.9		0.0
Turdus rufitorques	72.0		672.5				672.5		0.0
Melanotis hypoleucus	63.8	63.8	1042.8	63.8	548.8	0.0	494.1	0.0	494.1
Vermivora chrysoptera	8.8	79.2		44.0		35.2			
Parula superciliosa	8.5	25.5	89.3	0.0	53.6	25.5	35.7		0.0
Dendroica fusca	7.3	7.3	8.5	0.0	8.5	7.3			
Oporornis tolmiei	11.4	22.8	66.5	0.0	66.5	22.8			
Geothlypis poliocephala	11.0	11.0		11.0		0.0			
Wilsonia pusilla	7.9	15.8	18.4	0.0	6.1	15.8	12.3		0.0
Myioborus miniatus	8.8	114.4	102.7	70.4	34.2	44.0	68.5	44.0	68.5
Basileuterus rufifrons	11.3	11.3		0.0		11.3		11.3	
Basileuterus belli	10.7	32.1	1124.3	0.0	713.6	32.1	410.6	32.1	410.6
Chlorospingus ophthalmicus	17.8	35.6	4134.9	35.6	3786.0	0.0	348.9		0.0
Euphonia elegantissima	15.0		175.1		164.8		10.3		0.0
Chlorophonia occipitalis	25.8		60.2		60.2				
Volatinia jacarina	8.5	17.0		0.0		17.0			
Sporophila torqueola	8.0	16.0	18.7	0.0		16.0	18.7	16.0	18.7
Tiarias olivacea	9.0	18.0	31.5	0.0		18.0	31.5		0.0
Diglossa baritula	9.0	27.0	94.6	27.0	33.8	0.0	60.8	0.0	60.8
Haplospiza rustica	15.6		54.7				54.7		0.0
Atlapetes gutteralis	34.8	34.8	1259.6	0.0	514.4	34.8	745.3	34.8	745.3
Buarremon brunneinucha	44.3	88.6	3620.1	44.3	2127.9	44.3	1492.2	44.3	1492.2
Melozone biarcuatum	30.8	61.6	107.9	0.0		61.6	107.9	61.6	107.9
Aimophila rufescens	36.5	1022.0		693.5		328.5			
Zonotrichia capensis	17.2	34.3	200.3	0.0		34.3	200.3	34.3	200.3
Ergaticus versicolor	10.0	70.0		0.0		70.0			
Spizella passerina	20.3	40.6		0.0		40.6			
Saltator atriceps	79.7		558.5		55.8		502.7		0.0
Dives dives	96.2		224.7				224.7		0.0
Quiscalus mexicanus	149.0		3652.1				3652.1		0.0
Carduelis notata	11.0	33.0	141.3	0.0	33.2	33.0	108.1		0.0
Carduelis atriceps	19.8	19.8		0.0		19.8			
Sum:		39398.0	78031.0	16486.6	40973.4	22911.4	37057.6	3279.6	7055.4

Fat and muscle classes are correlated with each other (parameters muscle versus fat classes, linear regression: $y = 0.6919\,x + 1.25$, $r^2 = 0.59$). An individual increasing body mass will invest in both muscle and fat reserves. Individual recaptures showed no changes concerning fat and muscle classes (78 individuals).

As shown in Figure 30, body mass and individual numbers were correlated neither exponentially ($y = 11.96\,e^{-0.0119x}$, $r^2 = 0.19$) nor linearly ($y = -0.16\,x + 27.96$, $r^2 = 0.07$). One general pattern in body mass distribution might be that uncommon species have a higher body mass than common species. However, mist nets select species not by individual numbers but by behavior, vertical stratification, and other factors. Species with low body mass and infrequent captures might be rare in the study plot due to various different traits.

Several small species (body mass below 50 g) have high abundances while larger individuals are generally less abundant (Figure 30).

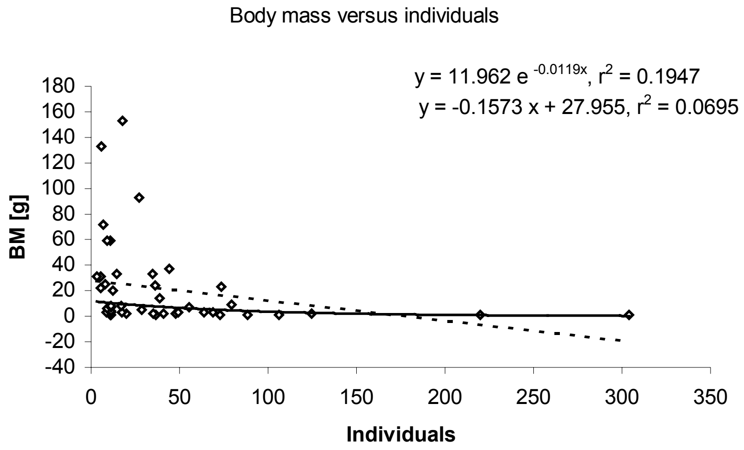


Figure 30: Regression (dotted line: linear, solid line: exponential) between number of individuals per species and body mass (g) in Chelemhá.

5.4 Morphometrics

All morphometrics in combination (bill length, width, height; wing length; total length; inner and outermost rectrices; tarsus) were analyzed using a MANOVA to distinguish between natural forest and young secondary forest. This might indicate that the two habitats are different, here in terms of size as a measure of fitness. The analyses included 596 individuals of 18 species. Here, too, 23 groups were established; for *Diglossa baritula*, *Lampornis amethystinus*, *L. viridipallens*, *Lamprolaima rhami*, and *Turdus infuscatus* a sexual separation for analyses was essential due to significant differences between the sexes. The morphometrical differences are not significant between the habitats (MANOVA, independent variable: habitat, $p > 0.50$). This might be explained with the genetic determination of size and natural variation. No spatial patterns are visible, which means that there are no significant traits between the two habitats and therefore no species is (e.g.) larger or smaller in any of the measured morphometrical parameters in natural forest or young secondary forest.

5.5 Syntheses

The differences in species numbers in both habitats are obvious. Independent of the method and the indices used there is a higher species number in young secondary forest, approximately twice as high as in natural forest. This was contrary to the expectations: I hypothesized higher species numbers in the natural forest (e.g., Karr 1971) of the study plot in the Sierra Yalijux.

Differences found between natural forest and young secondary forest were manifested in body mass as well as in the distribution of understory birds, heterogeneity, evenness, and species richness. The conclusions about the effects that human impact has on natural forest and its inhabitants is discussed in the following Chapter and compared with other studies in the region (Guatemala, Central America), the Neotropics and other tropical areas, and implications for conservation and the "value" of the natural forest of the Sierra Yalijux will be examined.

Most important are the differences between the two methods: while mist netting provided higher species numbers in young secondary forest, transect censuses showed that most species are more abundant in natural forest (Table 7).

The most abundant species – Common Bush-Tanager *Chlorospingus ophthalmicus* – is considered to be distributed in both habitats roughly equally using mist netting data. But a closer look at the transect census counts shows that *Ch. ophthalmicus* has most detections in natural forest, while in young secondary forests there are hardly any (213 versus 20 estimated individuals per 100 ha). The same is true for *Basileuterus belli* (67/38), *Lampornis amethystinus* (70/23), *Turdus grayi* (59/10), *Zimmerius villissimus* (39/10), and *Myadestes unicolor* (46/9). Further examples for the differing sensitivity of species to habitat are given in Table 10.

The differences might be explained by (i) differing frequency of individuals in the two habitats, (ii) larger number of individuals in natural forest due to more vertical strata and therefore more "space" for several species (e.g., *Ch. ophthalmicus* is distributed equally in all three vertical stratification classes used in section 5.2.13), and/or (iii) higher displaying and singing activity in natural forest. Regarding (iii), it is unlikely that there is higher singing and displaying activity in natural forest because in both habitats the standardized effort to count the individuals was equal. It is more likely that the differences in individuals is explained by the larger volume of habitats. Natural forest is up to tenfold higher and has more vegetation layers than secondary vegetation (Chapter 4.3) and therefore may harbor more individuals. Nevertheless, this does not explain the higher abundance of understory birds.

Table 10: Estimated individuals per 100 ha and captures per 12 net lines in the Chelemhá plot for total $N \geq 10$ captures.

	TOTAL		NF		YSF	
Species	N	TC	N	TC	N	TC
Colibri thalassinus	31	12	2	0	29	12
Lampornis amethystinus	126	93	76	70	50	23
Lamprolaima rhami	62	19	52	14	10	4
Henicorhina leucophrys	28	57	19	49	9	9
Myadestes occidentalis	22	36	1	12	21	24
Myadestes unicolor	13	55	8	46	5	9
Catharus frantzii	63	68	41	52	22	16
Turdus infuscatus	23	19	17	12	6	7
Turdus plebejus	9	23	5	19	4	4
Basileuterus belli	39	105	24	67	15	38
Chlorospingus ophthalmicus	148	232	57	213	91	20
Diglossa baritula	45	11	8	4	37	7
Atlapetes gutteralis	23	36	2	15	21	21
Buarremon brunneinucha	31	82	6	48	25	34
Total number of species:	64	75	32	56	57	64

N: captures with mist nets in Chelemhá. TC: individuals estimated with transect census techniques (ind./100 ha).

6 Discussion

6.1 Methods

6.1.1 Nets and transects

Both of the methods applied have advantages and disadvantages. Terborgh *et al*. (1990) suggested a combination of several methods to census tropical lowland bird communities adequately. Here, most of the same methods were used (standardized spot mapping and mist netting) to compare results and to test if the study plot has similar affinities like lowland rainforests or is more likely to be compared with subtropical or even temperate bird communities (compare Verner & Milne 1990, Poulsen 1994, Bierregaard & Stouffer 1997).

Mist nets are highly selective due to (i) the position at the ground (ii) the orientation of the 12 m net (it might be vertical or parallel in relation to flight corridors of territorial birds) (iii) behavior of the near ground living birds (iv) different visible capacities of birds. Even the recaptures are difficult to compare because certain species might be able to relocate the nets once captured and hence avoid them, while others cannot. “Net shyness” was once observed in young secondary forest in a hummingbird (*Colibri thalassinus*). The individual was marked by tail clipping. Once captured it was observed several times above the mist net located in the flying corridor and after closing the net it kept the same above ground altitude as if the mist net was still set. Verner & Milne (1990) found that spot mapping results are dependent on the observer (70 % of variance was explained by the observer) and not necessarily on differences in vegetation.

However, mist nets are not suitable to census a complete set of species or determine site tenacity because the bias is unreasonably high (further discussion in Karr 1981, Terborgh *et al*. 1990, Remsen 1994, Remsen & Good 1996, Bierregaard & Stouffer 1997). The most common species in the study area – *Chlorospingus ophthalmicus* – is censused by mist nets in roughly equal numbers in both habitats. Considering transect census, *Ch. ophthalmicus* is likely to be more abundant in natural forest with tenfold frequency. Many species show a similar pattern (compare Table 10 and Chapter 5.5). Reasons for this might be the different singing and displaying behavior and/or the larger amount vertical strata and therefore, generally more space and territories. The latter territories would not be distributed vertically as is usual, but instead, horizontally. Finally, the latter theoretical approach must be tested and verified.

In particular, hummingbirds (Trochilidae) with their comparable high visibilities are believed to see mist nets in advance (Karl-L. Schuchmann, pers. comm., Stiles & Wolf 1970, Snow 1983) or avoid mist nets, once captured. Both aspects are dependent up on the species: while *Lampornis amethystinus* was recaptured several times (R^t = 0.23), *Lamprolaima rhami* was hardly recaptured at all (R^t = 0.06). The first captures of hummingbirds are governed by the same pattern as all other species. There is one dominant and several rare species and there are species with higher or lower recapture affinities. Nevertheless, both species of hummingbirds are trap-liners and the individual turnover is high. *L. rhami* recaptures were not recaptured a second time. While the first number of captures equal each other in frequency, only one individual was observed in 2001 and 2002. Further aspects of recaptures and recapture rates are discussed in section 6.2.5.

Transect census techniques record species and individuals more accurately, but there are species with weak voices which are underestimated using this method. In particular, *Buarremon brunneinucha* and *Diglossa baritula* are detectable from no more than 25 to a maximum of 40 m distance.

6.1.2 Diversity indices and species-abundance models

As stated by several authors it is not useful to calculate all the possible indices and compare the results of the calculations (Whittaker 1972, Magurran 1988, Krebs 1999, Hondong 2003). Both, Sørensen indices and Bootstrap were used. Both are conservative estimators and successfully used before. Jackknife is better than Bootstrap for lower abundances (Magurran 1988). Bootstrap is used for larger samples and more accurate in this case than Jackknife. Moreover it seems to be the most suitable index for the study plot in Chelemhá.

The new indices ACE and ICE are presented here to show possible inadequacies. They were established by Colwell & Coddington (1994) because Chao 1 and Chao 2 underestimated species numbers steadily. Here, they proved to be a failure because overestimates were disproportionately high. The purpose is not to criticize overestimation, but because of its high incidence compared to Bootstrap by ACE and ICE, either the index does not serve the purpose of estimating the species numbers accurately or the investigation is not designed to meet the requirements (sufficient size and time, standardized methods, etc.).

Below, other indices were used (like α of log series, Shannon-Wiener) to compare the study site's diversity with other sites in Panamá, the Andes, Amazonia and western Africa (see section 6.3).

6.1.3 Neotropical and Nearctic migrants

Neotropical and Nearctic migrants play an important role in conservation, especially species threatened in North America. However, here they are neglected mostly due to sporadic appearances, except for *Wilsonia pusilla* and *Oporornis tolmiei*. The purpose of the study was to make an inventory of the resident species and compare them with different sites, also to compare the two major habitat types and the residents habitat preferences. Nevertheless, the habitat used by migrating species is of interest for North American conservationists because the conservation of many migratory species depends on the wintering habitat (e.g., Karr 1971).

6.2 Diversity

6.2.1 Species richness, diversity and evenness

The observed versus expected species number (Chapter 5.2.1) has a relatively high divergence. This is surely an effect of sampling and not all expected species will be present in the study plot or even in the region. The high differences between expected and observed species numbers might be a clue about several possible extinctions. One prominent species – *Oreophasis derbianus* – has already vanished. A prediction of extinctions and extinction rates was made in Chapter 6.6.1.

According to Terborgh *et al.* (1990) censusing a 102 ha large study plot is an adequate area to inventory 99 % or more of all present species in tropical landscapes. The fact that the Chelemhá plot covers more than two completely different habitat types acknowledges that both habitats were censused sufficiently to have 95 % of the species present.

α of log series (a diversity measurement; compare Magurran 1988) in Chelemhá is 15.95. In natural forest it is 8.06 and in young secondary forest 15.80. Terborgh *et al.* (1990), Thiollay (1994a, 1994b) and Robinson *et al.* (2000) do not provide any values for α of log series. Poulsen & Krabbe (1998) provide α for high altitude bird communities in Ecuadorian Andes. Values are between 15.2 and 20.7 depending on latitude within Ecuador and is comparably high.

α of log series is an old index of diversity (Magurran 1988). Waltert (2000) measured α in the Forêt Classée de la Bossematié in Côte d'Ivoire with 47.1 – 48.9 in the control area. Tropical lowland forest have higher diversity than the montane cloud forest in Chelemhá (see section 6.3 also).

Diversity, species richness and evenness measures of the Chelemhá plot are summarized in Table 11. As all indicators show, diversity and species richness is lower in natural forest. Several studies (e.g., Hughes *et al.* 2002) found similar patterns, but reproduction (i.e. source or sink habitat) is not necessarily proved, see below.

Table 11: Diversity and species richness in Chelemhá. α of log series from Krebs (1999), Singletons, Doubletons, Jackknife, Bootstrap, and ACE after Colwell (2000).

	total		natural forest		secondary vegetation	
Index	N	TC	N	TC	N	TC
Number of individuals (*N*)	865	1493	368	955	497	538
Number of species (*S*)	64	75	31	56	55	63
Singletons	19	10.79	8	0	16	6
Doubletons	13	6.61	8	3	13	4
α of log series	15.95 (± 3.98)		8.06 (± 2.10)		15. 80 (± 4.54)	
Diversity:						
Jackknife	81.50 (± 5.12)	86.27 (± 5.55)	41.17 (± 1.54)	55.09 (± 5.30)	72.83 (± 5.39)	66.89 (± 4.10)
Bootstrap	72.62 (± 2.73)	78.09 (± 1.54)	36.35 (± 0.77)	50.15 (± 0.00)	65.17 (± 0.00)	62.60 (± 0.00)
ACE	84.19 (± 8.50)	82.11 (± 2.58)	40. 56 (± 4.61)	46.00 (± 1.47)	72.43 (± 6.48)	61.86 (± 2.13)

N: mist netting, TC: transect census. For further explanations see text and for formulas see Chapter 4.5.

Heterogeneity of young secondary forest birds is higher in Chelemhá than in natural forest, nevertheless this might be considered to be forced by the steadily high degree of disturbance in the latter habitat. Furthermore, in largely cultivated areas like parts of North America or in Central Europe (where hardly any natural or natural-like forests are left) diversity is generally higher than in the presumed natural vegetation of oak-beech (e.g., Mühlenberg & Slowik 1997).

6.2.2 Vegetation structure and birds

That there is a connection between vegetation structure and abundance of species has been reported several times (e.g., Pearson 1975, Hinsley *et al.* 1995, Robinson & Terborgh 1997, Milberg *et al.* 2002, Walther 2002, Confer *et al.* 2003). For instance, understory species like *Henicorhina leucophrys* need dense understory or *Lampornis amethystinus*, which need relatively light understory structures (Chapter 5.1). Renjifo (2001) analyzed the influence of the surrounding landscape matrix on forest avifaunas. He stated that there is an influence on the forest avifauna from the surrounding landscape matrix. In Table 12 resident species with obvious vegetation and habitat preferences are listed.

Factor-analyses of four vegetation parameters gathered in the Chelemhá plot and species numbers per point (Chapter 5.1) yielded no significant results. Species densities of the Chelemhá plot are not dependent on the measured vegetation parameters. E.g., *Troglodytes rufociliatus* and *Henicorhina leucophrys* are crowding in localities where vegetation is denser than the surroundings.

Table 12: Habitat preferences of birds in the Chelemhá plot. x: observed in the relevant habitat during transect counts. #: from Stattersfield *et al.* (1998). (x): indicates possibly reduced or excluded reproduction.

Habitat: Species:	NF	PO	E	DU	SV	C
Ortalis vetula	x	x				
Penelopina nigra	x		x	x		
Cyrtonyx ocellatus		x		x		
Columba fasciata	x	x			x	
Bolborhynchus lineola	x					x
Strix fulvescens	x	x				
Colibri thalassinus					x	
Lampornis viridipallens	x	x	x			
Atthis ellioti	x	x			x	
Trogon mexicanus	x	x			(x)	
Pharomachrus mocinno	x	x			(x)	
Asphata gularis	x	x			x	
Aulacorhynchus prasinus	x					
Picoides villosus	x	x			x	
Colaptes auratus	x	x			x	
Automolus rubiginosus	x	x	x		x	
Grallaria guatimalensis	x	x		x		
Cyanocorax melanocyaneus	x	x			(x)	
Cyanolyca pumilo	x	x			(x)	
Notiochelidon pileata	x	x			x	
Thryothorus modestus				x		
Troglodytes musculus				x		
Troglodytes rufociliatus				x		
Henicorhina leucophrys				x		
Myadestes occidentalis	x	x				
Myadestes unicolor	x	x			x	
Catharus aurantiirostris	x	x				
Catharus frantzii	x	x			(x)	
Turdus infuscatus	x	x			x	
Turdus plebejus	x	x				
Turdus grayi	x	x			x	
Turdus rufitorques	#	#	x		x	
Melanotis hypoleucus	x	x			x	
Atlapetes gutteralis				x		
Buarremon brunneinucha				x		
Zonotrichia capensis					x	
Saltator atriceps					x	
Dives dives					x	
Quiscalus mexicanus					x	
Carduelis notata					x	
Carduelis atriceps	x		x		x	

NF: natural montane cloud forest; PO: pine-oak; E: forest edge/clearings; DU: dense understory (vegetation); SV: secondary vegetation; C: canopy.

6.2.3 Understory birds

Terborgh (1980) and Bell (1982) found that bird density is highest in the first 10 m above ground and at approximately 30 m vegetation height and lower in-between. Species numbers between 10 and 25 m is a third of the species numbers near the ground and the lower canopy (Terborgh 1980, Bell 1982).

Excluding higher strata species in young secondary forest due to vertical stratification, i.e. reducing the species numbers in young secondary forest, will be risky. The position of the investigator might influence the inventory and the detection of silent or quiet overstory species. In this case, the species are biased incorrectly and evaluation of the vertical stratification is poor. In the worst case, excluded species should be included and vice versa. Especially silent or quiet canopy species run the risk of being ignored. Perhaps there will be a differing understory species inventory when the position of the observer is at mid or higher levels. Due to methodological difficulties this effect is impossible to test.

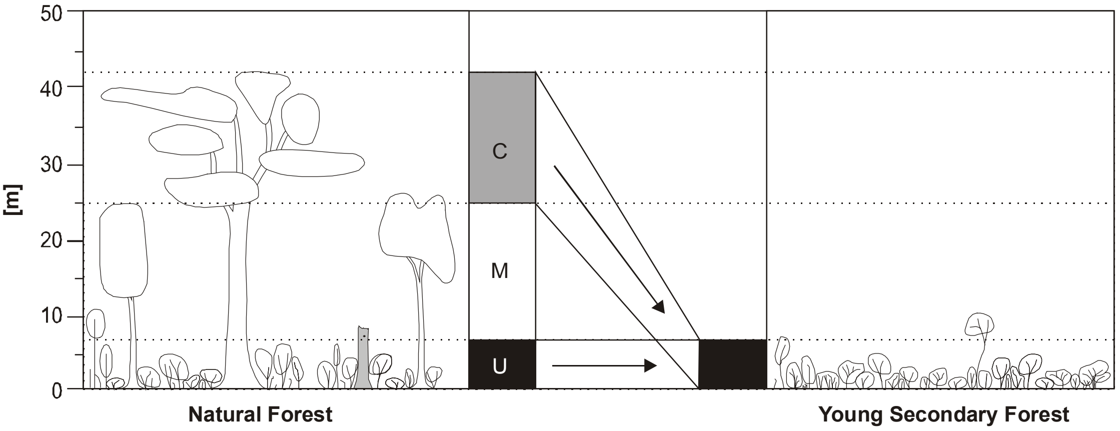


Figure 31: Theoretical background for understory birds and organization in natural forest and secondary vegetation. C: Canopy and overstory, M: mid layers, U: understory. Birds from canopy and mid layers move partly into secondary vegetation when natural forest is changed into human used secondary habitats or will disappear from secondary vegetation completely.

Waltert (2000) discussed the problems of the vertical mobility of overstory birds which are independent of the height difference between individual and ground (*cf.* Bierregaard & Stouffer 1997, Figure 31). Forests with low canopy might inhabit the overstory species but will bring them to heights which are capturable with mist nets. E.g., species in Chelemhá exclusively detected in high stratum in natural forest were captured in young secondary forest with a maximum tree height of 10 m. This was the reason for the exclusion of several species from diversity analysis (Chapter 5.2.12). Particularly for singletons or species observed only a few times ($N \leq 3$), stratification assignment was difficult or impossible. Conservative exclusion of questionable species was carried out.

Figure 32: The effect of exclusion from species classified as non-understory birds in the young secondary forest area of the Chelemhá plot. In an iterative process, species with no and/or unclear vertical distribution were excluded from observed species, Jackknife and Bootstrap estimator of species richness. A: all captured species included B: only presumed understory species included C: singletons excluded (observed species with one capture in young secondary forest) D: doubletons excluded (observed species with one or two captures in young secondary forest) E: $N \geq 5$ excluded F: only species with clear understory preferences were included.

The influence of exclusion from non-understory birds in secondary vegetation is illustrated in Figure 32 for observed species, Jackknife and Bootstrap. All three parameters show that canopy and overstory birds exclusion reduces diversity and species richness to a third of the original value. Variance between the indices does not matter, independent of how many rare species or singletons/doubletons are not certainly understory or canopy species. After exclusion of "true" or all possible understory birds, the variance between the estimators is not different (B to F in Figure 32; Friedman ANOVA: $p < 0.59$, $\chi^2 = 1.059$, Coefficient of concordance = 0.088).

There is a significant difference in species richness between the "sampled" and the "true" understory birds (Chapter 5.2.7) in both habitats.

6.2.4 Edge effect

Terborgh *et al.* (1990), Bierregaard & Stouffer (1997), Cândido (2000) and others showed that there might be a forest edge effect on plant and animal species in Amazonia. Several species are influenced by spatial and temporal patterns of forest edges. Depending on the species considered, either declining or increasing abundances are detected. Renjifo (2001) explains that any landscape matrix (i.e. the surrounding habitats of a forest) has an influence on the bird community within the relevant forest.

The edge effect in Chelemhá is relatively unmarked and not significant. While the natural forest avifauna is relatively homogenous and characterized by comparably low numbers of species and individuals, young secondary forest shows high fluctuations in both species and abundances (Figure 17). While the edge effect concerning species richness is not significant, the different species inventories show at least some kind of effect, independent from distance to the forest edge.

6.2.5 Recaptures and recapture rate

Recaptures were distributed over both habitats. While there were 12 species exclusively recaptured in natural forest, six were in young secondary forest. Seventeen of the 25 species captured in both habitats had a higher recapture rate in young secondary forest. First time recaptures do not indicate better habitat quality in natural habitats within the study plot in Chelemhá.

Before focusing on recapture rates, the different sensitivity of nets and transect census techniques is described: *Basileuterus belli* and *Myadestes unicolor* were not recorded sufficiently by nets. Discrepancies between the maximum (the important and comparable value of the iteration of Jolly-Seber) and the transect census population is comparable for most species, except for *Lamprolaima rhami*, *Diglossa baritula*, *B. belli*, and *M. unicolor*. The obvious differences are based on methodological sensitivity to special groups. *D. baritula*, *L. rhami* are underestimated by transect censuses. The calls of the hummingbird *L. rhami* are weak and are not carried over a distance of more than 25 m. The maximum detection distance of *D. baritula* lies between 25 m to a maximum of 40 m. *Buarremon brunneinucha* has a similar weak voice. The latter species is underestimated by mist netting because the ground living species has good vision. There were several records that the species may see the nets even in dark understory without the influence of light. *B. belli* and *M. unicolor* on the other hand are not recorded by mist netting completely due to habitat and vertical strata distribution. The latter species is exclusively recorded at strata above 10 m, mostly in the high canopy. The first species was observed frequently in mid-levels of vegetation. Neither were recorded sufficiently by mist nets.

Impact on tropical avifaunas is frequently estimated with recaptures (e.g., Lambert 1992, Johns 1992, Holbech 1996, Dranzoa 1998). Optimal habitats are usually correlated with high captures and/or recaptures and pessimal habitat quality with low captures and/or recaptures. Winker *et al*. (1995) showed exceptions of that rule with a simple graphic model (Figure 34). Winker’s model presumes that intraspecific competition in territorial birds forces subdominant (in the behavioral context) individuals to occupy suboptimal or pessimal habitats with increasing population density. Optimal habitats should be occupied by mainly territorial and dominant individuals. Waltert & Mühlenberg (2001) confirmed that *Andropadus latirostris* in Côte d’Ivoire show the same pattern. They found that captures in human used habitats were higher, but recaptures were lower in the same habitats. They concluded that a high recapture rate might be a good parameter for habitat quality.

Recapture rate is a measure of immigration/emigration and mortality/reproduction. These four parameters determine the size of a local population (Begon *et al*. 1996, Hanski 1999, Hanski & Ovaskainen 2000). Low recaptures of a species indicates high individual turnover and high territoriality (Table 13). Assuming that the method has no influence on mortality, the recapture rate is not affected because both marked and unmarked mortal individuals are contributing the same amount to the total meta-population and thus, to the recapture rate. The same is assumed for emigration, supposing that both marked and unmarked individuals have the same likelihood of emigration. On the other hand, immigration and reproduction is influencing the recapture rate of the local population because unmarked individuals are lowering the total rate of recaptures. Reproduction might be recognized by the proportion of captured immature individuals, if distinguishable.

Table 13: Theoretic effect of population parameters on recapture rates.

R^t	mortality (M^p)	immigration (I^p)	emigration (E^p)	reproduction (R^p)	individual turnover (^iTO)	territoriality (T_i)	method[1]
high	o	+ unmarked pop. - marked pop.	o	o[2]	-	+ -[3]	-
low	o	+ unmarked pop. - marked pop.	o	o[2]	+	-[3] +	+

+: positive (increasing) effect on recapture rate, -: negative (decreasing) effect on recapture rate, o: no effect on recapture rate.
R^t: recapture rate (recaptures per first capture) determined by population parameters (e.g., high immigration decreases R^t); [1] influence of captures on individuals by method, i.e. few individuals will disappear from the study plot or avoid nets, [2] post-breeding period, [3] if net avoided. ^iTO: turnover rate of individuals, i.e. the results of all four previously mentioned parameters (M^p, I^p, E^p, R^p).

Mortality, emigration and reproduction effects on both marked and unmarked individuals and hence has therefore no effect on recapture rates (Table 13, Figure 32). Reproduction has no effect in post-breeding marking procedures, whereas there is an effect during breeding season on the populations.

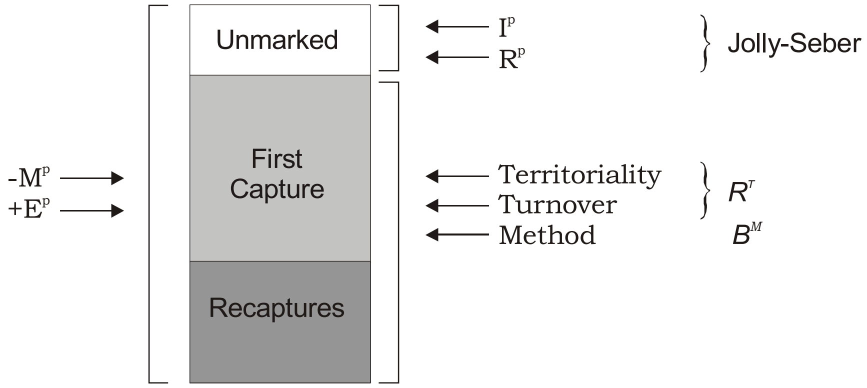


Figure 33: Theoretic effect of population parameters on the marked and unmarked population. R^t: recapture rate, B^M: influence of method is measurable by mortality during mist netting, M^p: mortality, I^p: immigration, E^p: emigration, R^p: reproduction.

The column "method" in Table 13 was added to show that the method may by no means influence single individuals (influence is not tested on birds today except for net avoidance, net shyness). Some individuals will avoid the net site after first capture, others might disappear from the study plot completely. The direct mortality of individuals that died within the nets or during measuring procedures in Chelemhá was lower than 1.0 %. It remains open, how many individuals died after releasing, as a result of capture procedures.

Waltert & Mühlenberg (2001) also discussed the importance of the recapture rate. They concluded that a high recapture rate of a species indicates a high proportion of territorial individuals or a long stay of individuals within the same area, i.e. a low individual turnover. As shown in Table 13 and Figure 33, individual turnover rate, territoriality and method have an effect on recapture rate.

As illustrated in Figure 33, the total population can be determined with the Jolly-Seber estimator (further explanations in chapters 4.5.6 and 5.2.8). The estimation of mortality and emigration of a population is barely possible to determine with the methods used in this study. It is unlikely that mortality for post-capture procedures can be determined in general, except for the directly observed death of individuals during mist netting and the observation of death of marked individuals in the field. No bird band was found or reported by locals in the community of Chelemhá. Emigration can be determined with a high degree of effort and large scale observations with e.g., color marked individuals. Territoriality and individual turnover can be determined by recapture rates and mortality rates ^{M}B (Table 13, Figure 33). Territoriality refers here to the proportion of individuals with and without territories, not the spatial extent of territories.

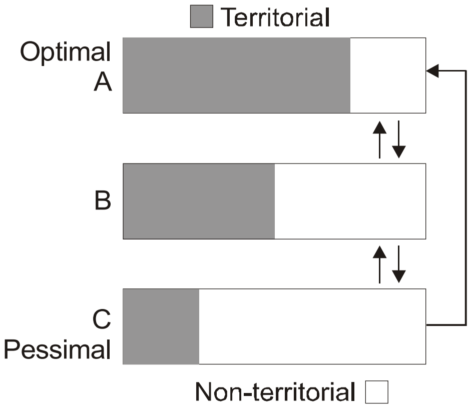


Figure 34: Model of non-territorial individual movements between optimal (A), sub-optimal (B) and non-optimal (C) habitats (adapted from Winker *et al*. 1995).

Presumably, if all of the following four parameters are valid, recapture rate can be a measure of habitat quality:

- the individual does not avoid nets after the marking procedure,
- recaptures are in some way proportional to territoriality ($T_i \sim r_i$) and negatively proportional to individual turnover ($T_i \sim -r_i = {}^{i}\mathrm{TO} \sim r_i$),
- methodological effects are determined and/or excluded (direct mortality during mist netting, ^{M}B),
- territories are more common in undisturbed and natural habitats (but see Winker *et al.* 1995).

Data for the three territorial species with sufficient recaptures are illustrated in Table 7. One major presumption for territoriality in Chelemhá was that the individual was first captured in 2001 and recaptured at least once in 2002 (in total, 16 species). It was further required that at least three individuals were recaptured once and a further three individuals were recaptured twice (r1 and r2 in Table 7; a total of 25 and eight species respectively) and at least one individual was recaptured three or more times (r3 and r4 in Table 7; a total of four species). *Catharus frantzii*, *Basileuterus belli*, and *Henicorhina leucophrys* were included and had a high degree of territoriality in the Chelemhá plot.

To calculate the unknown number of territorial individuals for the species is not promising because a control is difficult, if possible at all, due to low numbers and control of real territories. Therefore, the territories or homeranges of the species had to be checked by colored marking and observations or telemetry.

6.2.6 Population dynamics, influence of meta-populations and patchy distribution

Temporal and spatial dynamics are mostly neglected by the studies of tropical forest bird communities. Terborgh *et al*. (1990) and Robinson *et al*. (2000) gathered their data during one main breeding season within three months. Nevertheless, they had non-standardized data from more than one year, especially Terborgh *et al*. (1990) who sampled over several years at the Cocha Cashu plot. Neglecting temporal dynamics might give a wrong impression of the diversity and conservational status of the study plots. Studies in temperate regions showed that within a few years population size might change drastically. A well known example is the Snowshoe Hare in the Arctic (Begon *et al*. 1996) or the population dynamics of British breeding birds (Marchant *et al*. 1992). Bell (1982) reported seasonal differences in vertical distributions. Turchin & Ellner (2000) showed that the dynamics of voles are high and population estimates, even within one year, might be misleading.

Difficulties result from the patchy distributions of species (compare Thiollay 1986, 1988, Terborgh *et al*. 1990, own data) which also might change during time. Böhning-Gaese (1997) found that diversity measures are highly influenced by scale. Here, the 99 % threshold to measure the complete species set is guaranteed, according to Terborgh *et al*. (1990).

Hutchings *et al*. (2000) states that habitat (i.e. landscape, ecosystem) heterogeneity makes it difficult to give an accurate analysis of the community by short term investigations in combination with further temporal and spatial patterns (dynamics).

The meta-population concept of Hanski (1999; Figure 35a) and patchiness of distribution (e.g., Mühlenberg 1993) influences the observed number of individuals. Patchiness – simplified illustration in Figure 35b – influences the transect census techniques. While several patches might be situated within the study area, several species patches (i.e. meta-populations) might be situated partly within the plot or even outside. In the extreme latter case the species is not detected within the study plot. Species are distributed in patches and within the patches heterogeneously (Figure 35c). In the latter two cases, estimation of individuals or the observation of species numbers should be treated with caution. The latter effect is excluded by covering a sufficient area, and according to Terborgh *et al*. (1990) at least 100 ha will provide > 99 % of all species present in tropical lowland bird communities. While high altitudes are considered to be similar to high latitudes (e.g., Begon *et al*. 1996, Bergmann (1847) and annotation by Blackburn *et al.* 1999) it is more likely that the Chelemhá plot is observed sufficiently.

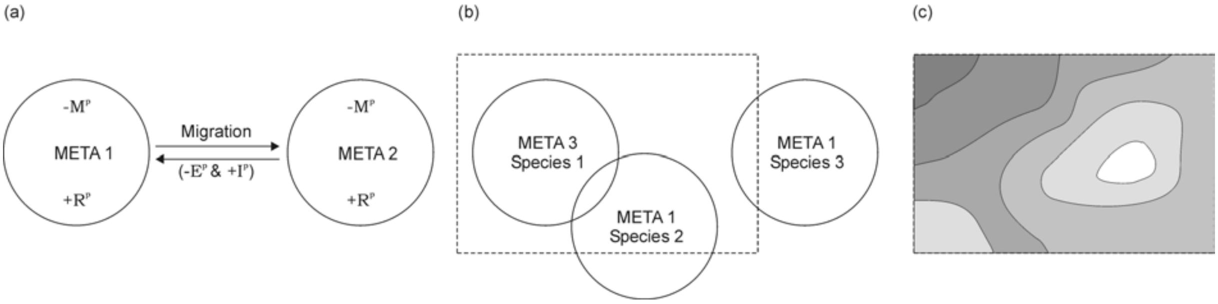


Figure 35: (a) The meta-population concept (simplified from Hanski 1999). (b) Influence of patchiness and meta-populations on census techniques. Dotted square symbolizing hypothetical sample area. (c) Heterogeneity of abundance of a hypothetical species, different gray colors indicate isoclines of similar abundance. M^p: mortality, R^p: reproduction, E^p: emigration, I^p: immigration, META: patch of meta-population (i.e. sub-population).

All these factors should be remembered when analyzing the data obtained. Nevertheless, the results are sufficient to draw scenarios for conservation and lead to real implications for management strategies. Nobody can help, even with years of investigation, if there are no suggestions for conservation and in the worst case, the study area is converted before any results are presented and the changes make any suggestions obsolete.

6.3 Comparison

Before focusing further on conservation in chapters 6.5 and 6.6, the bird community is compared with other plots worldwide.

Diversity and indices of diversity and its measures are a valuable tool to determine diversity on different levels (Magurran 1988; Rosenzweig 1995). It is useful to categorize and compare the study plots' diversity with other studies involved in avifaunal research. The (α-, β-) diversity of the study plot is basically compared to other measures of diversity in studies in Guatemalan cloud forests and lowland tropical rainforests, forests in tropical Central America, in the *Neotropis* (Neotropical mountains and lowlands) and last but not least in tropical areas of the *Orientalis* (Africa and south-east Asia). Other aspects like guilds, age structure, population sizes, etc. will be mentioned where methods were compatible. For all comparisons caution is necessary. In particular, methodological factors can lead to misinterpretation.

One central question is whether the bird community structure of the study plot in Chelemhá is more similar to tropical or subtropical climates than to those of temperate vegetation zones. It is questionable if the applied methods for bird census should be used as those in temperate forests (e.g., Karr 1971, Stiles 1973) which means less working effort for further studies or as those in tropical forest (e.g., Terborgh *et al.* 1990). While the first is involved with a combination of several standardized methods used mainly in non-tropical regions, the results of the tropical forest assessment will provide the overall results. Another possibility is to use methods applied such as in the high Andes (e.g., Ecuador; Poulsen &

Krabbe 1998), where more temperate climates are predominant. To answer the question, a combination of all methods used by Terborgh *et al*. (1990) was applied in this study to get the complete set of residents at the chosen plot.

Standardized bird censuses are rare in the tropics. First, Terborgh *et al*. (1990) suggested a combination of several methods applied in temperate forests to assess the spectrum of all bird species in a tropical forest. Within the Neotropics there are about three studies applying the same methods (Terborgh *et al*. 1990, Thiollay 1994b) and one in Central America (Robinson *et al*. 2000). Last but not least, studies were made in Côte d'Ivoire (Waltert 2000) and Gabon (Brosset & Erard 1986). The study plot in Chelemhá is another example of an attempt to census at least 99 % of all species.

6.3.1 Neotropical bird communities

The study of Eisermann (2000) was the first on bird communities in the Sierra Caquipec, 12 km west of Chelemhá. Some results are comparable due to similar methods and are presented below. This is the only study which partly resembles in methods and in altitude (1800 – 2500 m) the Chelemhá plot. All other studies presented below are located in lowlands below 1000 m elevation. The latter might influence comparison and falsify the results. Nevertheless, due to the lack of tropical highland study plots above 2000 m with comparable methods, comparisons with lowland studies were made.

In August 2003, Andrea Nájera started mist netting with the same sampling design as in the Chelemhá plot, in El Albores (15°07' N, 90° 05' W) at an elevation of 2500 m in the Reserve Biosfera Sierra de las Minas. The first few days of capturing birds indicate in general, a similar species set in Chelemhá and El Albores. But the most frequent species in Chelemhá (*Chlorospingus ophthalmicus*) was not recorded in El Albores, neither by mist netting nor by active searching for the species. Further results are expected in January 2004.

Cautionary note: *Apart from the difficulties of comparing lowland and highland, there are more factors which might influence or even prevent comparison between the sites. Intercontinental comparisons are questionable due to large differences between taxonomic groups. Even ecological patterns like spatial and temporal dynamics in populations and habitat heterogeneity influence the results.*

All studies mentioned in the following section include mainly natural forest but also some secondary forest. Depending on the study area, age and structure of the secondary forests differ.

The next study plot is located in Panamá (Robinson *et al*. 2000). Karr (1971) surveyed a 2 ha study plot, the so called Limbo plot, in lowland Panamá. The same 2 ha area was included by Robinson *et al*. (2000) and extended to 104 ha and standardized methods were applied, similar to Terborgh *et al*. (1990) in the Cocha Cashu plot.

A further two plots were located in the Amazon Basin, in Cocha Cashu, Perú (Terborgh *et al*. 1990) and Nouragues, French Guiana (Thiollay 1994b). Another study plot is located in the Forêt Classée de la Bossematié, Côte d'Ivoire (Waltert 2000). Species numbers, individuals, and if applicable, mass density (g/100 ha) are illustrated for all six plots in Table 14 and Figure 36. The Chelemhá plot and the plots in Cocha Cashu and Limbo are comparable by mass density pattern. While the latter two plots had a comparable density distribution, the Chelemhá plot differs in several relationships between the guilds. Fewer granivores and insectivores were represented in Chelemhá than at the other two sites, but nectarivores presented with a total higher mass in the first plot. Even the total mass is approximately twice as high at the Cocha Cashu and Limbo plots as in Chelemhá. Omnivores are represented in similar masses in all three plots. The different mass distributions per guild are most likely to be explained by the differing numbers of individuals (at least the Limbo plot had roughly twice as many individuals). Species numbers will not explain the pattern. Whilst the number of species in Cocha Cashu is three times higher, there are not a lot of individuals that are more represented here in relation to Chelemhá.

Table 14: Guild structure and density of birds (individuals) in different study plots in the Neotropics and western Africa. Illustrated are the resident birds (breeding and non breeding).

	Chelemhá[1]			Chicacnab[9]	Cocha Cashu[2]			Limbo[3]			Nouragues[4]	Bossematié[5]	
Guild[7]	*S*	*N*	mass density[6]	*S*	*S*	*N*	mass density[6,8]	*S*	*N*	mass density[6]	*S*	*S*	*N*
Aquatic	-	-	-	-	8	9.5	3075	7	13	3202	3	-	-
Carrion	-	-	-	-	1	0.5	600	3	3	4900	2	-	-
Frugivore	7	90	32 480.4	15	25	209	35 334	19	302	35 348	39	2	6
Granivore	12	172	7935.3	-[10]	22	180	79 630	10	77	58 972	8	5	27
Insectivore	31	467	9316.9	33	125	1063	34 144	113	2156	48 097	132	33	649
Nectarivore	9	149	871.2	10	11	44	227	12	131	644	15	5	241
Omnivore	14	597	25 974.6	27	35	302	21 295	56	653	32 807	29	3	279
Raptor	3	4	1452.5	11	18	48	8238	22	29	9179	22	1	5
Total	76	1479	78 031.0	96	245	1856	186 543	242	3364	193 199	248	49	1207

[1] 102 ha Chelemhá plot; [2] 97 ha Cocha Cashu, Amazonia, Perú (Terborgh *et al*. 1990); [3] 104 ha Limbo plot, Panamá (Robinson *et al*. 2000); [4] 100 ha Nouragues, Amazonia, French Guiana (Thiollay 1994b); [5] 110 ha Forêt Classée de la Bossematié, Côte d'Ivoire (Waltert 2000) mist net captures; [6] mass density of individuals per 100 ha (g/100 ha); [7] from Robinson *et al*. (2000); [8] g/100 ha, presented here for the 97 ha census plot; [9] species numbers (*S*) from Chicacnab (Eisermann 2000), illustrated are the presumed resident species without migrants, the total number of species in Chicacnab is 136; [10] not classified.
S: number of species; *N*: number of individuals, otherwise indicated; -: no observations.

Unfortunately, for the plots in Chicacnab, Nouragues, and Bossematié mass densities were not provided in definite numbers but in classes (Thiollay 1994b, Eisermann 2000, Waltert 2000; Figure 36). Nevertheless, it is possible to compare species numbers (here presumed residents) and for the latter site, individual numbers. The plot in Chicacnab, 12 km west of the Chelemhá plot, has a comparable number of species (96, of which 76 were presumed resident). Nouragues had three times more residents and totally observed species. Even the number of species per guild (note the unclassified guild of granivores in Table 14) in Chicacnab is differently composed from the Chelemhá plot. Chelemhá (and presumably Chicacnab too) is different regarding the most parameters from tropical lowland sites with standardized methods. Chelemhá in terms of bird community – as indicated by vegetation and climatic classification by Köppen and Holdridge – most likely belongs not to tropical, but to subtropical areas.

Terborgh *et al.* (1990) did not provide diversity indices for Cocha Cashu, Amazonia, Perú, only species numbers (Table 14). Residents were three times higher than in Chelemhá but comparable to the second site in Amazonia (Nouragues; Thiollay 1994b).

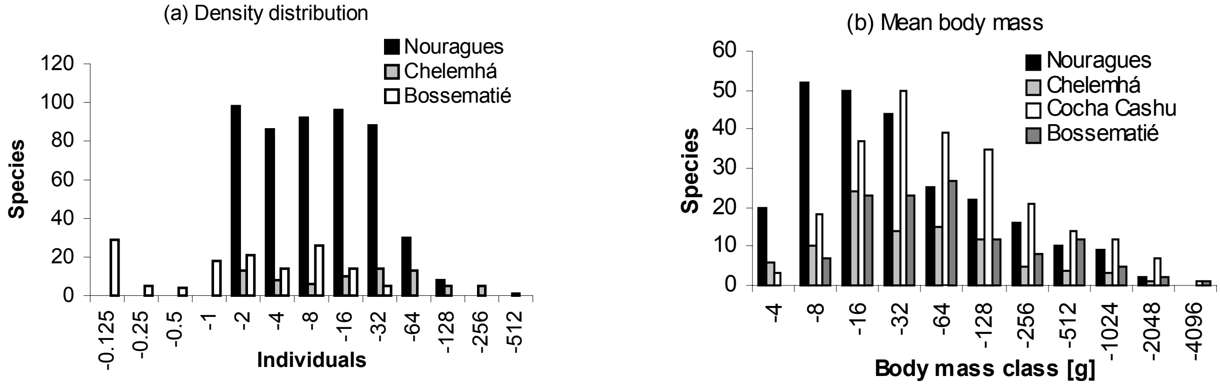


Figure 36: (a) Density (Individuals/100 ha) and (b) body mass distributions (g/100 ha) in Nouragues, Amazonia, French Guiana (Thiollay 1994b), Chelemhá (own data), Cocha Cashu (Terborgh *et al.* 1990) and Forêt Classée de la Bossematié, Côte d'Ivoire (Waltert 2000). Individuals and mean body mass axis were plotted on log$_2$ scale.

At the Nouragues plot (Thiollay 1994a, 1994b, 2003) in Amazonia of French Guiana 441, species were observed of which 248 were residents. The Shannon-Wiener was $H' = 4.957$, Evenness $E = 0.899$ and 52 % of all species were rare. Thiollay (1994b) defined rare as < 2 pairs/100 ha. Applying the same definition – changing rare to < 4 individuals/100 ha – to the Chelemhá plot, 42 % of all species are rare. Evenness E in Nouragues is near one, which means that all species are more or less equally abundant. Chelemhá has an $E = 0.62$ and $H' = 3.10$, both lower than in Nouragues.

Mean body mass distribution (Figure 36b) in three Neotropical study plots show that medium to small classes are more frequent. Large and small species are less frequent, especially in south-western Amazonia and central Guatemala.

6.3.2 Further studies involved in tropical bird communities

A conglomeration of several studies involved in tropical – even high elevation – bird communities have been published. Due to non-standardized methods, no effort is made to compare the study sites qualitatively because the value of a comparison will be poor and not meaningful. However, a 110 ha study plot in the Forêt Classée de la Bossematié, West Africa, was established to census the bird community (Waltert 2000). A total of 136 residents with 1418 individuals in natural forest and logged regeneration area (five years regeneration time after the last logging period) were observed. This resembles roughly the total number of species in the Chelemhá plot (see above).

Shankar Raman (2001), Shankar Raman & Sukumar (2002) and Shankar Raman *et al.* (1998) studied the effect of slash-and-burn agriculture on a bird community and analyzed the diversity of recovering secondary forests. They concluded that a secondary forest of ten years or older may preserve similar diversity as natural forest.

Poulson & Krabbe (1997, 1998) counted the bird communities of forest habitats at five study sites (each of 1 km²) in highland Ecuador between 3000 – 3350 m along a latitudinal gradient. Due to differing methods a comparison is barely possible, nevertheless some parameters are presented here. Poulson & Krabbe (*ibid*) observed between 42 and 58 species (S_{obs}) and between 224 and 321 individuals (N) depending on their study site. Both individuals and species numbers are lower in highland Ecuador than in the Chelemhá plot. They estimated log series α between 15.2 and 20.7. α of log series natural habitats is lower in Chelemhá than in Ecuador (8.06 versus 15.2). Evenness $E = 0.9$ in Ecuador is higher than in Chelemhá with $E = 0.62$ (natural forest). The latter indicates that abundance of species is more equal in Ecuador than in Chelemhá.

6.3.3 Bird communities in non-tropical regions

MacArthur *et al*. (1966) found that α-diversity in tropical forests is truly higher than in temperate areas. Karr (1971) compared four temporal and seven tropical lowland bird communities in Illinois (USA) and Panamá. Apart from methodological differences and difficulties, (e.g., singing males do not necessarily represent a territory of a breeding pair in tropical landscapes), there were large differences in species numbers between the plots. Tropical rainforests in Panamá had less residents (here breeding species), but the forest bird community was more diverse, had more and additional insectivores and different distribution within strata. Karr (*ibid*) mentions that 1.46 times more birds reside in tropical areas than in temperate areas. Terborgh *et al*. (1990) gained a value of diversity that is four to five times as great as would be found in any uniform habitat type in temperate North America.

The question of whether the bird community of the Chelemhá plot belongs to temperate or tropical bird communities is difficult to answer, but with regard to species numbers (S_{obs}) and the climatic classification, it is not tropical but subtropical or temperate (Chapter 4). The differences are most likely due to altitudinal and longitudinal traits.

Karr (*ibid*) compared the 2 ha Limbo plot in Panamá with different habitats in Illinois, North America. He sampled grassland, shrub and lowland forest in both the tropics and the temperate sample plots and drew comparisons. Differences between the two major ecosystem types are significant and obvious. Due to different methods, results are not comparable with the Chelemhá plot (2 versus 102 ha; different effort of mist netting; different spot-mapping methods) and classification is not useful if Chelemhá is more likely to be temperate or tropical in regard to Karr's investigation.

6.3.4 Differences between natural forest and young secondary forest

Differences between the two major habitats are the basis for the discussion of human impact on biological diversity. Simplified, natural forest is considered to be the control or unimpacted area, young secondary forest is impacted area. By mainly expanding slash-and-burn agriculture the natural forests are reduced steadily.

As shown in Chapter 5, several patterns are distinguishable between the two major habitat types (natural forest and young secondary forest). Other than general ecological patterns like diversity, body mass density distribution and recapture rates, species specific traits indicate better habitat quality in natural environs.

All applied indices indicate that diversity in young secondary forest is higher than in natural forest. Observed and estimated (ACE, Bootstrap) indices give generally higher species numbers in young secondary forest. At first, this seems astonishing, but by extracting species with non understory preferences and migrants, species richness roughly resembles each other in both habitats. Secondary habitats in northern temperate climates have generally less diversity than natural habitats (e.g., Hughes *et al*. 2002, Benton *et al*. 2003).

Hughes *et al*. (2002) summarizes that ecologists assume that young secondary forest (secondary habitats) do not have the same carrying capacity as natural forest for species in relation to species-area models. But if tropical countryside is managed properly, it may provide a substantial opportunity for tropical bird conservation. Half of all species are restricted to forest. The question remains open whether species reproduce in secondary habitats successfully.

Recapture rates and body mass density indicate that natural forest is advantageous to young secondary forest concerning bird communities.

6.3.4.1 Guild composition

As described in Chapter 5.4.2 (Figure 9c, 9d), guild composition shows differences between the two habitats in the Chelemhá plot. Focusing on the results gathered with transect census techniques, there are obviously more insectivore species in natural forest than in young secondary forest. While in both habitats the individuals number is comparably low, in the latter habitat there are relatively fewer insectivore species. The natural forest has a higher potential to carry different specialized insectivore species. Omnivores show a different pattern: they are present with roughly an equal percentage of species numbers in both habitats. But here there are many more individuals in natural forest than in young secondary forest. This indicates that natural forest might carry more individuals than young secondary forest with, at the same time, similar quality of nutrition sources.

6.3.4.2 Is body mass a measure of habitat quality?

Differences in total body mass per habitat indicate the different qualities of habitats. If considering specialization on nutrition, each individual and species will use its best area for feeding (Winker *et al*. 1995). Pessimal habitats will not provide sufficient food for all species because non-territorial individuals will crowd there. A poor food supply will cause mean lower body mass in the pessimal habitat. In Chelemhá this certainly is the secondary vegetation (see above and Chapter 5.3).

6.4 Biogeographic affinities

Of the 28 families observed in Chelemhá, most species belong to Trochilidae, Turdidae, and Emberizidae (Figure 37). Most families are represented with one or two species. This pattern is comparable to the species abundance models, where one species has many individuals and many species have few individuals. The difference is that at the family level there are three comparable frequent groups, see above. Analyzing the individuals/family relationship there is one family (Turdidae) with the absolute highest frequency followed by two comparable high frequent families (Thraupidae, Trochilidae; Figure 38).

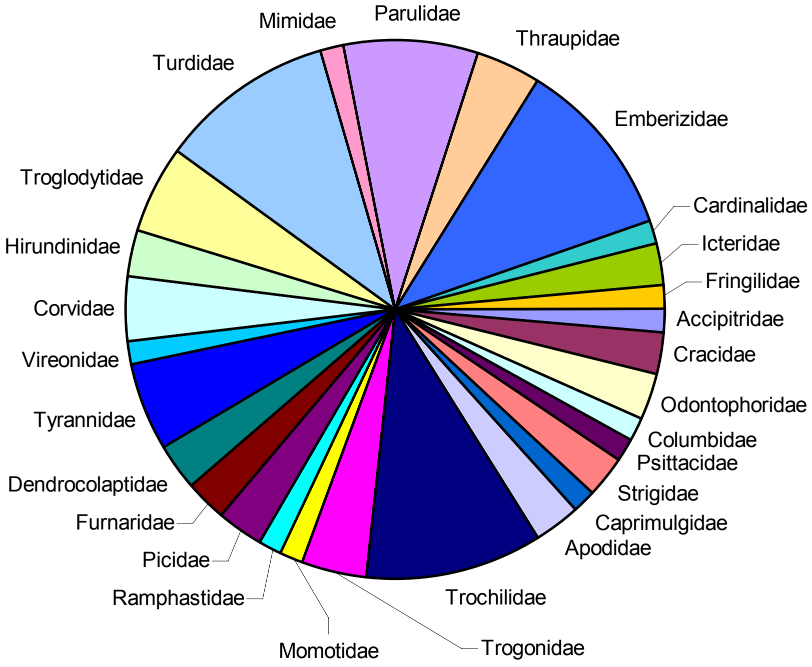


Figure 37: Percentage of species per family in the study plot of Chelemhá. Included are all transect census detections.

Dilger (*in lit.*) explained that the Yucatán lowlands were used by the Maya cultures for approximately 10 000 years. But the highlands, especially the mountain ridges of the Sierras Yalijux and Caquipec were not settled before the end of the 19th century. Until then, small scale disturbance occurred only naturally. Human impact was low until the 1950s. The lowland avifauna was possibly used to the human induced disturbance (nearly all of the Yucatán peninsula was used), but the northern most highlands of Guatemala were not influenced heavily. The latter, in combination with the recent heavy human impact, might be an indicator that the bird community is poorer than expected because the recent impact has already drawn several species to extinction.

To analyze the influence of zoogeographical regions, family origin was analyzed. Information was difficult to obtain and the family records by Howell & Webb (1995) were used. The relation of members of species per family in North and South America was compared. While Cracraft (1973) believed that the Trochilidae originally speciated in North America, several authors located the origin of this group in northern South America (e.g., del Hoyo *et al*. 1999). This is most likely considering the Trochilids center of species richness in the northern Andes. Table 15 summarizes the distribution in continental categories. Most families in the study plot are cosmopolitan (15) or Neotropical (13), none is exclusively Nearctic nor Central American. This indicates that the bird community is most likely to be tropical and Neotropical. The lack of North American entities is a result of exclusion of migratory species. This should not be overemphasized, because the few Nearctic migrant species will not change the general pattern.

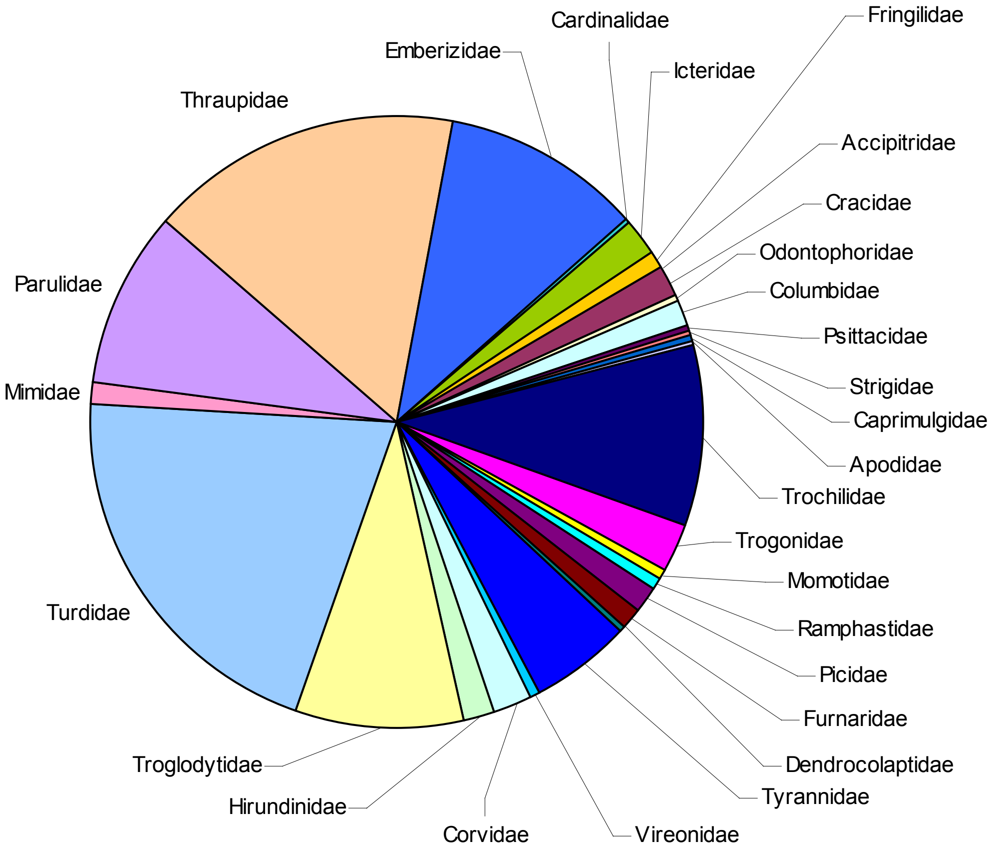


Figure 38: Percentage of individuals per family in the study plot of Chelemhá. Included are all transect census detections.

The interface between the *Neotropis* and *Nearctis* is somewhere in Central America or southern North America depending on the examined group (plants or animals, birds or mammals or arthropods etc.; Cox & Moore 2000). This also depends on the authors; Wehner & Gehring (1995) used the Río Grande between Mexico and the United States, Cox & Moore (2000) used the Río Balsas north of the Isthmus of Tehuantepec between both zoogeographic regions. However, the avifauna in Guatemala consists of both elements because the connection between North and South America is comparably young. The gap between both parts of the tectonic plate was closed comparably recently and the Isthmus of Panamá was closed during Miocene, approximately 8 million years ago (Weyl 1980, Lundberg *et al.* 1998).

Paleorefuges (refuge *sensu* Haffer 1974) in lowland Amazonia were postulated for areas with a high degree of endemism. Species are believed to have expanded and speciated from there into regions with today's lower species richness surrounding the paleorefuges. Within the area of the Andes and Cordilleras of Central America, the paleorefuges shifted altitude since the rise of the Andes/Cordilleras when climatic changes occurred. This is one explanation for a high frequency of endemics, presuming there are species promoting barriers like geographic barriers (Mayr 1999).

Evolutionary speaking, the bird community is comparably young (see above, Cox & Moore 2000) and mixed between the two intruding geographic compartments of *Neotropis* and *Nearctis*. Moreover, the bird composition is influenced by global warming up and cooling down periods and resulting vegetation shifts gave access to the region to species which were formerly restricted. Species were limited by sea level, shift of vegetation and climate.

Ecologically speaking, the comparably young – even younger than the evolutionary traits – disturbances (see above; Dilger *in lit.*) in lowlands might not bother many species. But specialists will be effected (see below), especially highland specialists with low experience of broad scale disturbance and less impact than in lowlands.

Table 15: Genera, species and individuals per family and their continental affinities (source: Howell & Webb 1995).

Family	Genera	Species	Individuals	*Nearctis*	CA	*Neotropis*	Cosmopolitan	Pantropical
Accipitridae	1	1	1				x	
Cracidae	2	2	22			x		
Odontophoridae	2	2	5				x	
Columbidae	1	1	20				x	
Psittacidae	1	1	6			x		
Strigidae	2	2	2				x	
Caprimulgidae	1	1	5				x	
Apodidae	2	2	5				x	
Trochilidae	7	8	139			x		
Trogonidae	2	3	37				x	x
Momotidae	1	1	8			x		
Ramphastidae	1	1	8	x	x	x		
Picidae	2	2	19				x	
Furnaridae	2	2	19			x		
Dendrocolaptidae	2	2	4			x		
Tyrannidae	4	4	77	x	x	x		
Vireonidae	1	1	8	x	x	x		
Corvidae	3	3	28				x	
Hirundinidae	2	2	25				x	
Troglodytidae	3	4	131	x	x	x	(x)	
Turdidae	3	8	301				x	
Mimidae	1	1	16					
Parulidae	6	6	137	x	x	x		
Thraupidae	3	3	246			x		
Emberizidae	8	8	153				x	
Cardinalidae	1	1	7				x	
Icteridae	2	2	27	x	x	x		
Fringilidae	1	1	13				x	
Total:	67	75	1467	6	6	13	15	1

CA: Central America; (x) few species are cosmopolitan distributed, main distribution in America.

6.5 Human impact

As described in Chapter 5, more detailed natural forest and young secondary forest are distinctive on different levels – diversity *sensu lato*, guild composition, body mass and trophic aspects. It still remains open how human impact should be evaluated in respect of ongoing deforestation.

As indicated in Chapter 5, the study plot in its total follows a lognorm distribution and is most likely to be not heavily disturbed. This evaluation is cautious because even if the influence is low, at least there is some human disturbance in the study plot. The latter aspect is especially the case in secondary vegetation as well as in natural forest.

Assuming, deforestation continues at a similar current rate, natural forest will be completely vanished in the study area within approximately 60 years (own estimation on basis of the medium Guatemalan deforestation rate, mainly in lowlands; Markussen 2003, Voigt 2003). Forest will be replaced by slash-and-burn agricultures mixed with the dead stump remnants of old oaks and pines. Like before, several species will disappear from the study area. *Alouatta pigra* and even the contemporary most common species *Chlorospingus ophthalmicus* will vanish from the study plot. The latter species is recorded with transect census techniques in both habitats and while it is frequently captured in both habitats it is more likely that it is more common in natural forest (Chapter 5.5).

Slash-and-burn agricultures cannot provide the complete set of species in a region compared to natural forest. Only ten year or older secondary forest (Shankar Raman 2001) has the carry capacity to potentially hold a major species set. The secondary forests in Chelemhá are younger than five years. The human impact on natural habitats is enormous. Studies involved in tropical regions do not provide any information on whether secondary vegetation might have a similar carrying capacity for diversity (“biodiversity”) in the tropics.

Murphey (2003) and Peterjohn (2003) stated that only under special management and recreation terms can secondary habitats possibly support range extensions or biodiversity (Benton *et al*. 2003). Greenberg *et al*. (1997, 2000) stated that coffee and cacao plantations – even with shading trees – have no or less value for birds and birds species richness. Unfortunately, secondary habitats in the Chelemhá plot fail to support diversity and hence biodiversity. Even if the diversity in secondary habitats at a first glance seems to be higher, secondary habitats are not suitable to preserve biological diversity for several species of higher conservation interest like *Alouatta pigra* or *Pharomachrus mocinno*.

As long as human population in the study area (and within the tropics as a whole) is steadily increasing the need for more agricultures increases too. Alternative incomes to subsistence agricultures are not available and as long as the educational system is not improved will not be available.

6.6 Conservation of natural montane cloud forest in the Sierra Yalijux

Examining human impact and differences between disturbed and undisturbed forest has consequences for the conservation of the bird community and the remaining forest fragments of the Sierra Yalijux.

6.6.1 Predicting extinctions

Spatial diversity (species-area relationship) patterns have important implications for conservation of biodiversity and understanding these patterns contributes to our knowledge of community structure.

Species and area are related with $S = cA^z$, where S number of species, A area, z and c constants (e.g., MacArthur & Wilson 1967, Rosenzweig 1995, Krebs 1999, Waltert *et al.* 2003).

The inverse species-area relationship (Preston 1962) might assess the number of extinct forest dependent bird species threatened from deforestation. This procedure has been proven to be valid since it produced results that were concordant with assessments of mammal and bird threat status made by conservationists. The observations were consistent both in Neotropical and south-east Asian tropical rainforest (Brooks & Balmford 1996, Brooks *et al.* 1999a, 1999b, 1999c, Brook *et al.* 2000, Waltert *et al.* 2003). Rearranging the relationship $S = cA^z$, one can calculate the number of species most likely to become extinct in a fragment (or nested subset) of a given size by dividing $S_{surviving} = cA_{surviving}^z$ by $S_{original} = cA_{original}^z$. This results in $\frac{S_{surviving}}{S_{original}} = \left(\frac{A_{surviving}}{A_{original}}\right)^z$ and one can estimate the extinct species $S_{extinct} = S_{original} - \left(S_{original} \cdot \left(\frac{A_{surviving}}{A_{original}}\right)^z\right)$, because $S_{extinct} = S_{original} - S_{surviving}$.

Assuming the regional meta-population of the Sierra Yalijux has no individual or genetic exchange (the next natural montane cloud forest is located in the Sierra de las Minas, 20 km southwards, separated by the valley of the Río Polochic), one can set $A_{surviving}$ to 55 000 ha (see methods for details) as the remaining natural montane cloud forest with $A_{original}$ = 165 000 ha for the Sierra Yalijux (Markussen 2003). The area of EBA # 018 Central American highlands is $A_{original}$ = 15 000 000 ha.

Focusing on the 21 natural montane cloud forest specialists endemic to the Central American highlands (Table 16, Stattersfield *et al.* 1998), 10 should be present in natural forest and oak-pine forests. Thirteen out of the 21 and six out of the10 were observed in Chelemhá (Table 16). Figure 39 illustrates the relationship between the 21 mentioned endemics and area, Figure 40 for the 10 natural montane cloud forest endemics.

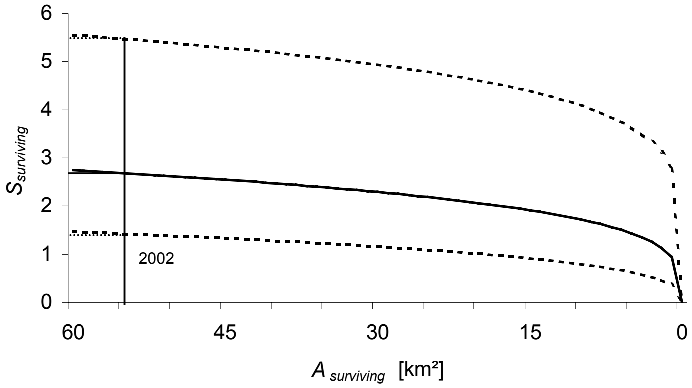


Figure 39: Relationship between 21 highland bird species of EBA # 018 remaining ($S_{surviving}$) and remaining closed forest cover within areas of the Chelemhá plot. Dotted curves represent calculations using extreme $z = 0.17$ and $z = 0.34$, respectively.

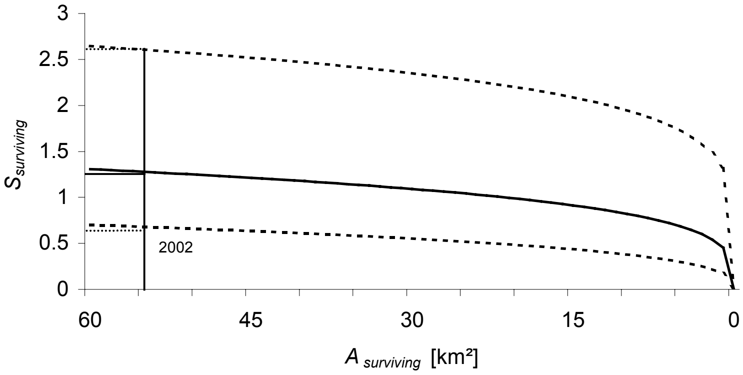


Figure 40: Relationship between 10 highland natural montane cloud forest bird species of EBA # 018 remaining ($S_{surviving}$) and remaining closed forest cover within areas of the Chelemhá plot. Dotted curves represent calculations using extreme $z = 0.17$ and $z = 0.34$, respectively.

According to the 21 endemics from EBA # 018 "Central American highlands" (Stattersfield *et al.* 1998) there will be 2.68 endemics remaining ($S_{surviving}$) for the remaining 5500 ha natural forest in the Sierra Yalijux. For extreme *z*-values, 1.4 and 5.47 endemics will remain, respectively. In contrast, 13 endemics were observed. Considering the 10 natural forest highland endemics, 1.28 are remaining ($S_{surviving}$) and six were observed in the Chelemhá plot (see Table 16). Therefore, a lot of more species are still present than might be carried by natural forest. So even when area is not decreasing and the deforestation rate will immediately be zero, four to five out of the six natural forest highland endemics will not survive because the area-species equilibrium is not reached!

Rosenzweig (1995) reviewed empirical work on species-area patterns and showed that the slope of the species-area curve (*z*) differs between nested subsets of habitat, real islands, small forest fragments and areas with different biogeographic history. Since there is no empirical data available on the species-area relationship for Guatemala, the traditional value of $z = 0.25$ (Preston 1962) has been chosen, which has also been used for archipelagos of islands as well as for larger forest fragments within islands (Brooks *et al.* 1997, 1999a). To obtain information on the robustness of the estimate, two “extreme” values of z (0.34 and 0.17) were also used to calculate $S_{extinct}$. While a high value such as $z = 0.34$ is almost certainly overestimating species loss, the low value of $z = 0.17$ underestimates threat (see also discussions of z-values in van Balen 1999, Brooks *et al.* 1999b, Waltert *et al.* 2003).

6.6.2 Endemics

Endemics (as defined here in close and fare endemics, Chapter 5.2.12) – or restricted range species – are mostly dependent on restricted habitat use in special areas. Centers of such areas with a higher degree of endemism are named Endemic Bird Areas (EBA in Stattersfield *et al.* 1998). Within Central America there are 30 EBAs. EBA 018 “North Central American highlands” is 150 000 km^2 large, 500 – 3500 m in elevation; key habitats are montane forest, pine-oak forest and deciduous forest which are threatened by moderate habitat loss. EBA 018 is classified as “Priority – Urgent”. Two of the 20 restricted range species of EBA 018 are threatened (*Oreophasis derbianus*, *Tangara cabanisi*), both were not present at Chelemhá or already extinct there. Nevertheless, 13 of the 20 restricted range species were recorded. Out of the 13, at least three were exclusively montane evergreen and pine-oak species (*Strix fulvescens*, *Lampornis viridipallens*, *Troglodytes rufociliatus*; Table 16).

Table 16: Endemic and specialized birds of the Sierra Yalijux and the Chelemhá plot. Listed are all species classified in the Endemic Bird Area 018 “North Central American highlands” adapted from Stattersfield *et al.* (1998).

Species	Global status[1]	Altitude (m)	Present in Chelemhá	Habitat[2]
Podilymbus gigas	extinct (1987)	1500	-	water
Oreophasis derbianus	vulnerable	2000 – 3000	extinct (~ 1990)	NF
Cyrtonyx ocellatus	near threatened	1000 – 3000	*	PO
Otus barbatus	near threatened	1800 – 2500	not recorded	NF, PO
Strix fulvescens	least concern	1200 – 3000	*	NF, PO
Campylopterus rufus	least concern	900 – 2000	not recorded	NF, PO, SF, e, a
Lampornis viridipallens	least concern	1400 – 2200	*	NF, PO, e
Lampornis sybillae	least concern	1400 – 2200	not recorded	NF, PO, e
Doricha enicura	least concern	1000 – 2200	*	NF, PO, SF
Atthis ellioti	least concern	1500 – 3500	*	NF, PO, SF
Asphata gularis	least concern	1500 – 3000	*	NF, PO, SF
Xenotriccus callizonus	near threatened	1200 – 2000	not recorded	deciduous forest
Notiochelidon pileata	least concern	1000 – 3000	*	NF, PO, SF
Troglodytes rufociliatus	least concern	1700 – 3500	*	NF, PO, e
Melanotis hypoleucus	least concern	1000 – 3000	*	NF, PO, SF
Turdus rufitorques	least concern	1500 – 3350	*	NF, PO, e
Tangara cabanisi	least concern	1000 – 1700	not recorded	NF, PO
Ergaticus versicolor	near threatened	1800 – 3500	*	NF, PO, SF
Icterus maculialatus	least concern	500 – 1800	not recorded	PO, SF
Carduelis atriceps	near threatened	2000 – 3500	*	PO, e, SF
Cyanocorax melanocyaneus	least concern	600 – 2450	*	e, PO, SF

[1] adapted from Stattersfield *et al.* (1998). Due to different nomenclature, differences to Table 17 may occur. [2] NF: montane evergreen forest, PO: pine-oak forest, SF: secondary growth, e: forest edge, clearings; a: agricultural areas, * observed in Chelemhá.

Possingham *et al.* (2002) stated that Red Lists are not designed (i) to set priorities for resource allocation for species recovery (ii) to inform reserve system design (iii) to constrain development and exploration and (iv) to report the state of the environment. On the other hand, Lamoreux *et al.* (2003) stated that the misuse is indeed given and agree with Possingham (2002) “(i)t is naïve and counterproductive from all point of views to use threatened species lists alone to allocate resources for recovery, …”. Therefore, several more aspects (habitat comparison, measure of influences, body mass, etc.) were integrated to evaluate the Chelemhá plot.

Fjeldså *et al*. (1999) analyzed the accuracy of EBAs in Africa and South America. They concluded that if protection of the EBAs “core areas” is given, at least 94.4 % of all species of the continent will be protected. However, those areas with remaining patches of natural vegetation are under intense human pressure.

6.6.3 Keystone and target species

Chelemhá has two species which are both suitable as target and flagship species for conservation: *Pharomachrus mocinno* Resplendent Quetzal and *Alouatta pigra* Yucatán Black-Howler Monkey. Their populations are still successfully reproducing, they are abundant and they are present in the mind of the peasants and the human population outside the study area. Last but not least, they represent the natural forest and the distribution is limited to Central America or the Yucatán Peninsula.

6.6.3.1 Resplendent Quetzal – *Pharomachrus mocinno*

Mühlenberg *et al*. (1989) recorded at least three viable populations in Guatemala (Sierra Cuchumatanes in the western highlands, effective population of 7200 individuals; Chelemhá, 5700 individuals; Sierra de las Minas, 27 000 individuals) and two more which might support viable populations (Chamá East, 4900 individuals, and Chamá West, 4500 individuals) but were not investigated sufficiently due to inaccessibility. The theoretic basis for the classification of the minimal viable population was 5000 individuals. They presumed 500 active reproducing individuals as the minimum number necessary (Hovestadt *et al*. 1991). Several correctional factors were added to assess the individual numbers of the minimal viable population: breeding success per male (2.5x), breeding success per breeding pair (2x) and variance in breeding pair success (2x).

Mühlenberg *et al*. (*ibid*) concluded that the minimal area for *Ph. mocinno* is 111 km² for 15 males/km² in Chelemhá (data resumed in the previous paragraph). Considering 33 males/km² as determined in the study of 1989, the minimum area needed for viable meta-populations with no presumed exchange of individuals (but compare Powell & Bjork 1994, 1995 for immature individuals) is 50.5 km². The latter value indicates (i) the presumption of 15 males/km² is too low, or (ii) the males are crowding within the forest remnants, or (iii) the local population of Chelemhá is condemned to extinction.

Unfortunately, the estimated minimum area is less than half of the remaining natural forest in Chelemhá and surroundings. Mühlenberg *et al*. (*ibid*) estimated the male population as 33 individuals/km² in Chelemhá in 1989. In 2002, the individuals were approximately 18 males/km², approximately half of the population of 1989. The differences can be explained by (i) methodological differences and/or (ii) natural population dynamics (see above).

Because of insufficient information on a species, it is difficult to evaluate the population viability. Even today, the situation is still not improved and knowledge about species like

Quetzals is poor. Habitat loss will overrun conservationists and many species will vanish without sufficient knowledge or not even be described by the scientific community (e.g., Terborgh 1999).

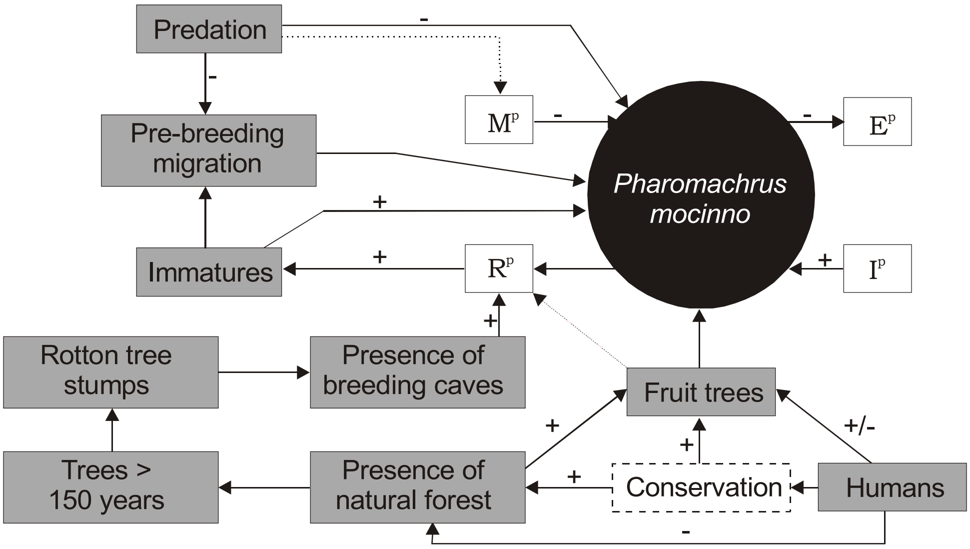


Figure 41: Factors influencing the population of *Pharomachrus mocinno* in Chelemhá. +: positive/increasing effect, -: negative/decreasing effect. M^P: mortality, E^P: emigration, I^P: immigration, R^P: reproduction success.

In 1973, a sanctuary to preserve the Quetzal was established at the southern slopes of the Volcano Atitlan (LaBastille 1973). Mühlenberg *et al.* (1989) concluded that the south-eastern slopes of the volcano were not suitable for *Ph. mocinno* and they did not detect any there. This discrepancy might be explained by the differing areas (south versus south-eastern) or that the populations are meanwhile extinct. When establishing reserves for Quetzals it is necessary to include the seasonal movements of immature Quetzals otherwise protection will be insufficient (Loiselle *et al.* 1989, Powell & Bjork 1994, 1995).

Population decline of *Ph. mocinno* is forced by habitat destruction by humans (agricultural expansion, slash-and-burn, erosion, etc.) and even by natural impacts like earth slides, fires, etc. (LaBastille 1974). Artificial nests might be a good alternative for natural breeding caves. In 50 % of the installations, artificial caves were accepted by female *Ph. mocinno*. However, breeding success was not proven.

The previous analysis of *Ph. mocinno* might be used as part of a population viability analysis (PVA) and basis for minimal viable population (MVP). Soulé introduced the procedure of a PVA in 1986 (Soulé 1986, 1987). The PVA is a method to determine the likelihood of survival of a local population within a previously defined period (e.g., 100 years). While dependent on species and local populations, the procedure has to incorporate different parameters. Applied to *Ph. mocinno* and *A. pigra*, estimation of survival for the next 100 years is directly linked to the presence of the reproducing habitat.

Compared to lowland rainforests, there are relatively many old rotten tree stumps left in the Chelemhá plot and in general in the cloud forests of the Sierra Yalijux. While in lowlands, especially in Africa, dead trees are used rapidly and almost instantly by termites (Isoptera) and do not remain for long. In the cloud forest of the Sierra Yalijux, termites are not present and ants (Formicaridae) are rare (own data). The presence might be limited, at least for termites, by the comparably lower temperatures below 0 °C . There was no observation of ants or termites during the study period, even though a careful search was undertaken. This might be a reason for rotten tree stumps remaining for several years and even decades, in the cloud forest.

Figure 41 illustrates the intrinsic and extrinsic factors determining the population size of *Ph. mocinno*. Beside the four common intrinsic parameters determining each population (immigration, emigration, reproduction, mortality), two major factors are believed to influence the population; the nutrition tree supply and the presence of breeding caves. The latter aspect is explained above. Fruit trees are present in all habitats and are not believed to drive the Quetzal into extinction (Unger 1988, Mühlenberg *et al*. 1989).

Breeding caves are limited by the existence of natural forests as they are exclusively reproduced there. The tree stumps will remain for approximately a further 50 years in slash-and-burn agriculture until they fall over.

6.6.3.2 Yucatán Black-Howler Monkey – *Alouatta pigra*

Beside the birds there are several mammals in the Sierra Yalijux which might support the purpose of conservation of the natural forests. E.g., one prominent primate species in the Chelemhá plot was *A. pigra.* This species is added here, to show similar patterns from a different species group.

Alouatta pigra is exclusively abundant in natural forest or old secondary forest. The territories of the groups have two size classes in Chelemhá: groups with small areas (with 2.5 to 3.9 ha) and groups with large areas (4.6 to 7.6 ha). While the small groups had records with semi-adults and no juveniles, the larger groups had the complete set of distinguishable age stages. The first are believed to consist of young individuals grouping until adopted by territorial groups and the latter are reproductive entities.

A. pigra is a perfect target species in Chelemhá because with its successful protection a lot of additional species will be protected, too. Due to the need of natural, or at least old secondary vegetation (> 10 a), a lot of species will be protected in the name of *A. pigra*. Even *Ph. mocinno* will be included, if sufficient natural forest is protected.

This mammal species is an additional target and keystone species suitable for conservation.

6.6.4 Red Lists and extinction risk

No species represented in Chelemhá during the study period in 2001/2002 was listed by Red Lists (Groombridge 1993, Baillie & Groombridge 1996, Collar *et al*. 1992). Stattersfield

& Capper (2000) listed *Pharomachrus mocinno* Resplendent Quetzal as "Lower Risk/Near Threatened Species" (resembles category 2). Globally or continental wide this may be true and applicable, especially for *Ph. mocinno*. However, considering the study plot in Chelemhá, more species are threatened. Large birds like *Penelopina nigra*, *Aulacorhynchus prasinus* and *Ortalis vetula* and primates like *Alouatta pigra* are also threatened (for further species see Table 17). Considering the scenario of the population viability for *Ph. mocinno* and *A. pigra*, the additional two species mentioned above are also threatened by habitat loss. Even *Ch. ophthalmicus* should be considered as regionally threatened (Chapter 5.5).

The following species might be driven to extinction by humans in the next decades: *Pharomachrus mocinno*, *Alouatta pigra*, *Penelopina nigra*, and *Troglodytes rufociliatus* as endemics and *Chlorospingus ophthalmicus*, *Basileuterus belli*, *Lampornis amethystinus*, *Buarremon brunneinucha*, *Turdus grayi*, *Catharus frantzii*, *Henicorhina leucophrys*, *Myadestes unicolor*, *Zimmerius villisimus*, *Thryothorus modestus*, *Mitrephanes phaeocercus*, and *Turdus plebejus* as non endemics and resident birds in the Chelemhá plot. All mentioned species have more detections in natural forest than in secondary vegetation and their population will decrease drastically when natural habitats vanish.

Small species and forest specialists are particularly prone to habitat destruction (Cardillo 2003). Most insectivore species are specialized in natural forest nutrition spectra.

Table 17: Factors threatening selected species and their status in the Chelemhá plot in Guatemala, Central American highlands (CAH) and globally (Stattersfield & Capper 2000).

		Status[1]			
Species	Factor	Chelemhá	Guatemala	CAH	Globally
Ortalis vetula	habitat loss	2	–	–	–
Penelopina nigra	habitat loss and loss of reproductive areas, hunting	1	2	–	–
Oreophasis derbianus	habitat loss, hunting	0*	1	1	1
Cyrtonyx ocellatus	habitat loss and loss of reproductive areas	1	2	–	–
Bolborhynchus lineola	habitat loss	3	–	–	–
Trogon mexicanus	habitat loss and loss of reproductive areas	2	– (3)	–	–
Pharomachrus mocinno	habitat loss and loss of reproductive areas	1	2 (1)	2	2
Asphata gularis	naturally rare species in combination with habitat loss	3	– (3)	–	–
Cyanocorax melanocyaneus	reduced habitat quality in young secondary forest	3	–	–	–
Cyanolyca pumilo	reduced habitat quality in young secondary forest	3	–	–	–
Alouatta pigra	habitat loss and loss of reproductive areas	1	2	2	?
Panthera onca	habitat loss	1	2	2	?
Puma concolor	habitat loss	1	2	2	?
Total:		13	7/10	5	2 (5)

[1] Status categories (proposed status): 0: Extinct, 1: Near Extinction/Threatened Species (Endangered), 2 Lower Risk/Near Threatened Species, 3 Least Concern, – not threatened. * former presence and observations reported by locals.

6.6.5 Conservation strategy

If accepting the need for conservation (generally and particularly in the study area), a conservation strategy should be applied. The aim of the strategy should be to preserve the remaining natural forest patches. Some parts of this section are strongly simplified and by no means explained from the viewpoint of a conservationist committed to nature and its functioning. The needs of the local human inhabitants sometimes get lost, but are nevertheless necessary!

6.6.5.1 Factors threatening species and habitat

Several factors influence growth or decline of populations (compare Table 17). Besides natural factors, the most threatening is the human impact. Habitat destruction and conversion (here deforestation) is one of the major factors threatening or leading to extinction of local or whole populations (LaBastille *et al.* 1978, Long 1995).

As shown above, deforestation is influencing the bird populations enormously, not to mention vegetation structure or plant composition. It is most likely that other animal groups like mammals and insects are also influenced in terms of composition, diversity and abundance.

6.6.5.2 Possibilities to preserve the natural forest remnants

Generally, there is more than one single factor threatening species, habitats or whole ecosystems. Nevertheless, the main factor is habitat loss. Beside natural influences (natural fire, hurricanes, El Niño as possible human induced global climatic effect, etc.), human influence is still increasing and is one of the major factors causing deforestation. Human influence is the most facet rich component and factor for deforestation and/or habitat loss. Reasons for habitat loss in most cases, is agriculture to guarantee substantial incomes and food.

As long as humans and their activities are the major reasons for habitat loss it is worthwhile promoting alternative incomes for *campesinos* (peasants). Alternative incomes are usually urban or suburban, not rural, i.e. where the natural resources and natural habitats are located. Peasants tend to hesitate to migrate, except the younger people. Alternative incomes are expensive to install and in rural and so called undeveloped or underdeveloped areas, difficult to generate.

One possibility to promote alternative incomes in rural areas is ecotourism or ethnotourism. At the study area there are two examples, one in Chicacnab promoting ethnotourism and one comparable new project in Chelemhá promoting ecotourism. The first was established in 1995 by the Proyecto Eco Quetzal with the aim of installing alternative incomes for the peasants. In the early stages of the project, large amounts of the project income was submitted to support administration (approximately 80 %). The situation changed in 2002, when some of the Chicacnab inhabitants decided to take on the responsibility of the project (own data). The success of the self-guided project is not reportable[3], but if successful the money will go where it should – to the locals. The second project was established in Chelemhá as part of so called ecotourism. Swiss immigrants bought natural forest to protect it. While the purpose of a *Reserva Privada* (reserve on private property with private

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[3] When visiting Guatemala few days before submitting the thesis in August 2003, the project was in responsibility of the Proyecto Eco Quetzal again and flourishing – the engagement of the locals was not accepted, neither by the Proyecto nor by the tourists.

responsibility, but with official status) is useful to protect the area, the income from the ecotourism project is gathered by the owners and the income of the locals is not improved. Here, ecotourism protects indirectly by financing the *Reserva Privada*.

From the viewpoint of a conservationist advocating nature (here defined as functioning of natural processes *sensu* Terborgh 1999), the best way to preserve the forest remnants is to get humans out of the forest as much as is possible and justifiable with regards to humanity.

The existing conservation strategy should be transmitted into action. One part of the strategy is the previously mentioned ethno and ecotourism projects. Further actions are to promote fruits like strawberry and plums, just like other crops and agricultural products in the study area. The problem here is (i) the acceptance of the peasants (acceptance is partly high) (ii) sometimes the peasants are not taught to use and plant the products satisfactorily, consequently they become disinterested and the products are lost (iii) organizations (non-governmental organizations, NGOs) have several problems like high turnover of staff, lack of resources and inadequate knowledge and experience.

The pine-reforestation program of the Guatemalan authorities was installed to prevent rural communities to continue with deforestation and to give alternative timber resources (Armin Schumacher, pers. comm.). *Pinus maximinoii* is planted in at least 16 ha areas. The plantations are expected to yield sufficient timber in 25 to 30 years. The problems are the large scale monocultures which are susceptible to pests and the high investments. The latter is not usually acceptable for peasants.

However, to evaluate and document the success of the conservation strategy it is highly recommended to observe the populations (birds, mammals, arthropods, etc.) and to alert authorities or NGOs if changes occur.

6.6.5.3 Priority areas and corridors: existing strategies

Priority areas were suggested to cope with the fact that many natural habitats will vanish in the future, most of them in tropical landscapes (Myres *et al*. 2000, Moore *et al*. 2003). The aim is at least to save nature in the proposed areas. Mostly, they are equated with a high degree of endemism in the tropics (e.g., Moore *et al*. 2003). To guarantee genetic exchange the priority areas, at least, should be linked with corridors of similar habitat. Haddad *et al*. (2003) found no evidence for use or acceptance of corridors. This is not astonishing because several corridors for forests and highland species are located within non-forest areas and/or cross valleys in Guatemala (MAGA 2001). However, in Guinea-Bissau (western Africa) corridors were accepted by larger animals, especially rhinos (Charlotte Karibuyo, pers. comm.).

Parks and protected areas prevent loss of “biodiversity” (Bruner *et al*. 2001). Bruner *et al*. (2001) used questionnaires, which does not necessarily mirror the real conditions in the parks and the parks administrators interviewed might color the real facts. Contrastingly, Terborgh (1999) is of the opinion that most parks are not suitable for keeping the functioning of natural systems and that many parks will not survive. Terborgh (*ibid*) questions whether most parks are large enough to stop species loss as a consequence of habitat loss, with respect to the theory of island biogeography (MacArthur & Wilson 1967 and others).

My own data shows that almost all parks in Guatemala have to cope with ongoing destruction and new human settlements.

6.6.5.4 Suggestions for a new strategy/extension of the existing strategy

The existing strategy and efforts to preserve the forest are a good basis for the conservation but must be translated into action. Otherwise, the natural forests will be prone to extinction.

6.6.5.5 Conservation of diversity within secondary habitats

Currently, there are several investigations testing whether secondary vegetation (e.g., Shankar Raman *et al*. 1998, Shankar Raman 2001, Shankar Raman & Sukumar 2002, Benton *et al*. 2003, Peterjohn 2003) is suitable for preserving species richness and “biodiversity”. Used as a background is the fact that in Central Europe, where hardly any square meter of primary or natural vegetation is left, the species numbers increased while humans converted natural beech-oak forest to a cultivated heterogeneous farmland habitat patchwork. Shankar Raman *et al*. (1998), Shankar Raman (2001), Shankar Raman & Sukumar (2002) observed similar species numbers and species sets in old recovering secondary vegetation. Farmland seems to be unsuitable to prevent biodiversity loss (Benton *et al*. 2003) when current intensification continues. However, secondary vegetation, except older recovering forest, is not a useful alternative because vegetation is rare and mainly used before the critical age is reached.

Weibull *et al*. (2003) compared organic with nonorganic organized farms in Sweden. Plants and arthropods were used. Species richness in agroecosystems of Sweden showed a connection between landscape matrix and diversity. But in comparison with natural or even primary forest, the study failed to present any results because no natural conditions as reference were used.

Salafsky *et al*. (1993) examined the impact of timber extraction on natural forests in Petén, Guatemala and Kalimantan, Indonesia. They concluded that extraction reserves are not the best, but are better than nothing to save rain forests. Socioeconomic conditions particularly influence the after extraction conservation of the forest. Diversity in coffee plantations is poor in Guatemala, compared to natural forests and traditionally cultivated coffee areas (Greenberg *et al*. 1997). To preserve high diversity in Guatemala or tropical areas, coffee plantations are not useful. Natural forests or old secondary vegetation may be the most promising way to preserve a high degree of diversity in the tropics.

One single study investigated the effect of tropical countryside on bird populations (Hughes *et al*. 2002). They concluded that if managed properly, the tropical countryside may provide a substantial opportunity for tropical bird conservation. They also stated that even if many bird species are reproducing in the countryside, in the absence of detailed population studies on every species, they cannot say whether these populations are sustainable, i.e. whether they are source or sink populations.

Brooks *et al*. (1999a, 1999b, 1999c, *cf.* MacDougall & Loo 2002) show that in tropical forest fragments isolated for more than 50 years, bird diversity is still declining. The time scale of regeneration in countryside habitats is unknown.

6.7 Conclusion

The forest remnants of the Sierra Yalijux, Alta Verapaz, Guatemala, are threatened to vanish due to human activities. From the viewpoint of a conservationist, they must be protected (*Reserva Privada*, Parque Natural) to avoid further reduction of natural forest area. This will be the only way to preserve the present abundant birds and mammals of the Central American highlands. The human population is the crucial factor threatening species, habitats and ecosystems. The combination of poverty, lack of education and diversity hotspots are critical (Cincotta *et al*. 2000).

For several species (birds: *Ortalis vetula*, *Penelopina nigra*, *Trogon mexicanus*, *Pharomachrus mocinno*, *Asphata gularis*, *Aulacorhynchus prasinus*, *Troglodytes musculus*, *T. rufociliatus*, *Chlorospingus ophthalmicus* and others; mammals: at least *Panthera onca*, *Puma concolor*, *Alouatta pigra*), the remaining natural forests will be not suitable to obtain viable populations for Central American montane cloud forests within the next 100 years. Moreover, it seems to be that some specialists prefer secondary habitats. This forces the question of whether secondary habitats are suitable or even more preferable for special species. However, several species like *Pharomachrus mocinno* and *Alouatta pigra* are dependent on natural or natural-like habitats in the Sierra Yalijux. This at least, is a sufficient reason to preserve the remaining cloud forests in central Guatemala.

The missing top predators are a hint that the forests in Chelemhá are too small to carry viable populations. Generally, the “value” of the forest is reduced for the bird community, but for single species like *Pharomachrus mocinno*, the value is still high.

The Chelemhá plot and comparable study plots in the Neotropics and western Africa generally show similar patterns (e.g., body mass distribution), but in detail are quite distinctive. Diversity, evenness and species richness differ and in parts resemble more temperate – subtropical bird communities. Guild pattern, species numbers and body mass distribution resemble more tropical study plots. The bird community of the Chelemhá plot is somewhere in-between.

Because scale and area matters (e.g., MacArthur & Wilson 1967, Rahbeck 1997, Rosenzweig 1995, Böhning-Gaese 1997, Krebs 1999, Rahbeck & Graves 2000) in diversity research it is necessary to standardize the study plot area. At least 100 ha should be sampled (Terborgh *et al*. 1990 and others) to get a complete set of birds. Studies involved in bird communities should emphasis the same area to make comparisons possible.

7 Summary

Structure and diversity of cloud forest bird communities in Alta Verapaz, Guatemala, and implications for conservation.

In a 102 ha study plot in the Sierra Yalijux, Alta Verapaz, Guatemala (90° 03’ W, 15° 22’ N, 1980 – 2550 m) the bird community was observed with standardized mark-recapture and transect census methods within natural and natural-like pine-oak cloud forest and secondary vegetation.

The study plot consists of two compartments with equal areas of natural (near primary) vegetation and young secondary forest (approximately 5 years old). The latter is a result from slash-and-burn agriculture. Special emphasis was made to analyze whether secondary vegetation is suitable to preserve a comparable amount of diversity of natural forest. Different approaches were made to test the differences. Diversity, species richness, evenness, body mass distribution, recapture rates, territoriality, guild structure, abundance of specialists and endemics were used to compare both compartments. Diversity and species richness were lower in natural forest than in young secondary forest. Of a total of 99 species observed within the 102 ha plot 63 were recorded in secondary vegetation and 56 in natural forest. However, evenness, body-mass distribution, recapture rates, territoriality, and abundance of specialists and endemics were higher in natural forest. Guild composition was significantly different between the two habitat types. Insectivorous birds were more frequent in natural forest in both species and individual numbers compared to secondary vegetation. Granivorous birds on the other hand, were more frequent in young secondary vegetation.

The body mass of birds was, both at the species and individual level, higher in natural forest than in young secondary forest because of the presumably better nutrition resources in the first habitat type. Recapture rates and abundance of birds were comparable higher in natural forest (955 individuals in the 51 ha part of the total study plot) than in young secondary forest (538).

Accordingly, young secondary forest is not suitable to preserve bird communities and avian diversity like in natural forests in a long term.

Central American highland endemics were mainly present in natural forest. E.g., the Resplendent Quetzal (*Pharomachrus mocinno*) will disappear after a relaxation time of 50 years following the complete destruction of the natural forest at the study site (own data). The population survival of this species in the long term is dependent on the rotten tree stumps with their breeding holes, which are absent from secondary vegetation.

Furthermore, the species-area-equilibrium for the Central American highland endemics (21 species in total from EBA # 018; Stattersfield *et al.* 1998) is not yet reached at the study site and ten out of the 13 observed endemics will vanish, even if destruction of the natural forest will stop immediately.

The bird community in the Chelemhá plot is in terms of species richness more similar to highland bird communities in Ecuador (e.g., Poulson & Krabbe 1997) or temperate sites in North America (e.g., Karr 1971) than to lowland Panamá (Robinson *et al.* 2000) and Amazonia in eastern Perú (Terborgh *et al.* 1990).

Because natural forest is advantageous to secondary vegetation in terms of abundance, overall body mass distribution, proportion of specialists and endemics, it is highly recommended that natural forest fragments in the Sierra Yalijux be preserved. In particular, for the long term persistence of the two target species, Resplendent Quetzal *Ph. mocinno* and Yucatán Black-Howler Monkey *Alouatta pigra*, the preservation of natural forest remnants is essential for long-term survival.

8 Zusammenfassung

Struktur und Diversität von Vogelgemeinschaften in Bergnebelwaldgebieten von Alta Verapaz, Guatemala, und deren Relevanz für Naturschutzstrategien.

In einem natürlichem und naturnahem Eichen-Kiefern-Bergnebelwald auf einer 102 ha großen Untersuchungsfläche in der Sierra Yalijux, Alta Verapaz, Guatemala (90° 03’ W, 15° 22’ N, 1980 – 2550 m) wurde die Vogelgemeinschaft mit standardisierten Fang-Wiederfang- und Transektzählmethoden erfasst.

Das Untersuchungsareal besteht aus zwei Bereichen, die zu gleichen Flächenanteilen Naturwald (primär) und jungen Sekundärwald (ca. 5 Jahre alt, hervorgegangen aus slash-and-burn-Subsistenzwirtschaft) einschließt. Der Schwerpunkt der Untersuchung wurde auf die Unterschiede zwischen beiden Habitattypen gesetzt, um zu analysieren, ob Sekundärvegetation in tropischen Landschaften geeignet ist, ein vergleichbares Maß an Diversität zu bewahren, wie es im Naturwald vorgefunden wird. Hierzu wurden Artenreichtum, Evenness, Körpermassenverteilung, Wiederfangraten, Territorialität, Nahrungsgildenstruktur und Abundanzen von Spezialisten und Endemiten statistisch analysiert und beurteilt. Während Diversität und Artenreichtum im Naturwald geringer sind als im jungen Sekundärwuchs, sind Evenness, Körpermassenverteilung, Wiederfangraten, Territorialität, Abundanzen von Spezialisten und Endemiten im Naturwald höher. Die Nahrungsgildenstruktur ist in beiden Habitaten signifikant verschieden, d. h. insektivore Vogelarten sind sowohl in bezug auf Artenzahl als auch Diversität im Naturwald häufiger als im Sekundärwuchs. Demgegenüber sind Granivore in Bezug auf die selben Parameter im Sekundärwuchs stärker vertreten. Dies verdeutlicht, das durch menschlichen Einfluss das Nahrungsangebot für Vögel in den zwei untersuchten Habitattypen verändert wurde und mehr granivore Generalisten in Sekundärhabitaten vorhanden sind, als im Vergleich zum Naturwald, der mehr insektivore Spezialisten aufweist.

Obwohl der Artenreichtum (insgesamt 99 beobachtete Arten in der Gesamtuntersuchungsfläche von 102 ha) in der anteiligen Sekundärvegetation des Untersuchungsareals (63 Arten) vergleichsweise höher ist als im Naturwald (56) ist dies aufgrund der weiteren gemessenen und beurteilten Parameter (s. o.) als negativ im Sinne des Naturschutzes zu bewerten, da in gestörten Habitaten der Artenreichtum in der Regel zunimmt. Die Körpermasse der Vögel ist sowohl auf Individuen- als auch auf Gesamtvogel-Biomassenniveau im Naturwald höher als im jungen Sekundärwuchs was auf die bessere Nahrungssituation im Naturwald zurückgeführt wird. Des Weiteren sind die Wiederfangraten und Abundanzen der Arten im Naturwald vergleichsweise höher als im Sekundärwuchs (538 Individuen im jungen Sekundärwuchs und 955 im Naturwald, jeweils in Bezug auf 50 % der Gesamtuntersuchungsfläche), und somit sind mehr Territorien im Naturwald vorhanden.

Aufgrund der untersuchten Parameter wird deutlich, das junger Sekundärwuchs nicht dazu geeignet ist, langfristig weitgehend naturnahe Strukturen der Vogelgemeinschaft zu erhalten.

Aufbauend auf die Daten der gesamten Vogelgemeinschaft wurde insbesondere die Situation in Bezug auf die Überlebensfähigkeit von Spezialisten und Endemiten genauer untersucht. Zentralamerikanische Hochland-Endemiten sind besonders im Naturwald anzutreffen und reproduzieren sich zumeist ausschließlich in diesem Habitattyp. So wird z. B. der Quetzal (*Pharomachrus mocinno*) mit der kompletten Zerstörung des Naturwaldes nach einer Relaxationsphase in der Region aussterben, da er ausschließlich in den charakteristischen Totholzbaumstümpfen brütet, die ausschließlich im Naturwald entstehen werden können.

Des Weiteren ist für Endemiten des Zentralamerikanischen Hochlandes (insgesamt 21 Arten der Endemic Bird Area # 018, nach Stattersfield *et al.* 1998) das Arten-Areal-Gleichgewicht noch nicht erreicht und selbst bei konstantem Naturwaldbestand werden noch zehn der 13 beobachteten Endemiten im Untersuchungsgebiet aussterben.

Im Vergleich zu anderen Untersuchungsarealen im Tiefland von Panamá (Robinson *et al.* 2000) oder dem Amazonasbecken (Ost-Perú; Terborgh *et al.* 1990) weist das 2500 m hoch gelegene Untersuchungsgebiet in Chelemhá deutliche Unterschiede auf: Der Artenreichtum ist geringer und gleicht anderen Hochland-Avifaunen wie z. B. in Ecuador über 3000 m (Poulson & Krabbe 1997) oder denen gemäßigter Breiten Nordamerikas im Tiefland (Illinois; Karr 1971). Evolutiv gesehen sind 13 der insgesamt 28 Familien neotropisch oder rein südamerikanische Elemente, 15 kosmopolitisch und nordamerikanisch.

Da Naturwald für die Naturschutzziele „besser“ in bezug auf Abundanzen, Körpermassenverteilung, Territorialität, und Anteil von Spezialisten und Endemiten als Sekundärwald ist, wird der Schutz der verbliebenen Naturwaldfragmente in der Sierra Yalijux als essentiell bewertet, da nur so Spezialisten und Endemiten langfristig vor dem regionalen Ausstreben gerettet werden können. Als Zielarten können Quetzal *Pharomachrus mocinno* und Yucatán-Brüllaffe *Alouatta pigra* herangezogen werden, da sie einerseits direkt vom Naturwaldbestand in langer Sicht abhängig und andererseits markant in Habitus und Verhalten sind. In Sekundärwuchs (jünger als 10 Jahre) kommt der Brüllaffe gar nicht vor und der Quetzal nur solange dort die typischen Totholz-Brutbäume noch übrig geblieben sind. Aus diesen Gründen ist der Schutz des verbliebenen Naturwaldes unbedingt erforderlich, um Arten wie z. B. den Quetzal langfristig vor dem Aussterben zu bewahren.

9 Resumen

Estructura y diversidad de la comunidad de aves en áreas de bosque nuboso de Alta Verapaz, Guatemala, y su relevancia para las estrategias de conservación

Se estudió la comunidad de aves en un bosque nuboso natural de pino encino, que se extiende en 102 ha en la superficie de la Sierra Yalijux, Alta Verapaz, Guatemala (90° 03' W, 15° 22' N, 1980 – 2550 m). El área fue analizada con métodos estandarizados de marcaje-recaptura y censo de transectos.

El área de estudio, Chelemhá, está compuesta de dos partes similares en superficie de bosque primario y de bosque secundario joven (parcelas de aproximadamente cinco años, originadas de la agricultura de subsistencia de tumba y quema).

La investigación estuvo enfocada a establecer las diferencias entre estos dos tipos de hábitats para analizar si la vegetación secundaria en los paisajes tropicales es capaz de conservar diversidad en forma comparable al bosque primario. Con tal fin, se juzgaron y analizaron estadísticamente diferentes parámetros, como diversidad (en sentido de heterogeneidad), riqueza de especies, equitatividad, distribución de biomasa, tasa de recapturas, territorios, estructura según la dieta, abundancia de especialistas y de especies endémicas.

Mientras que la diversidad y la riqueza de especies es más reducida en el bosque primario que en la vegetación secundaria, la equitatividad, distribución de masas, tasa de recapturas, territorialidad, y abundancia de especialistas y endémicos es más alta en el bosque natural primario.

La estructura según la dieta, difiere significativamente en ambos hábitats. Las especies de aves insectívoras son tanto en cuanto a número de especies como en cuanto a diversidad, más comunes en el bosque natural que en la vegetación secundaria. Por el contrario, las granívoras están más fuertemente representadas, en cuanto a los mismos parámetros, en la vegetación secundaria. Esto hace claro que por la influencia de las personas, la oferta de alimento para las aves ha cambiado en ambos tipos de hábitat, y que existen más granívoros generalistas en los hábitats secundarios que en el bosque natural, en donde se presentan más insectívoros especialistas.

Aunque la riqueza de especies (en total 99 especies observadas en toda el área de investigación de 102 ha) fue comparativamente mas alta en la vegetación secundaria (63 especies) que en el bosque natural (56), esto puede ser calificado, en virtud de otros parámetros medidos, como negativo, ya que regularmente en los hábitats perturbados, la heterogeneidad aumenta.

La masa corporal de las aves es tanto en cuanto a número de individuos como en cuanto a nivel de biomasa del total de aves, más alta en el bosque primario que en la vegetación secundaria, lo cual se debe a la mejor situación de alimentos en el bosque natural.

La tasa de recapturas y las abundancias de las especies fueron comparativamente más altas en el bosque natural que en la vegetación secundaria (538 en crecimiento secundario jóven, y 955 individuos en el bosque natural, correspondiente al 50 % de la superficie total de investigación), y con ello, se tienen más territorios en el bosque natural.

Debido a los parámetros investigados, se hace claro que la vegetación secundaria joven no es apta para mantener a largo plazo las estructuras naturales de la comunidad de aves. Con los datos obtenidos de la comunidad aviar, se investigó más específicamente la situación relacionada con la capacidad de sobreviviencia de las especies especialistas y endémicas. Las especies endémicas de las tierras altas de Centroamérica se encuentran principalmente en el bosque natural y se reproducen en su mayoría casi exclusivamente en éste tipo de hábitat. Así, especies como el quetzal (*Pharomachrus mocinno*) desaparecerán con la perturbación completa del bosque natural después de una fase de relajación en la región, debido a que ellos necesitan los característicos troncos de árboles muertos que solamente pueden reproducirse el bosque natural.

Para el resto de especies endémicas de la tierras altas de Centro América (en total 21 especues del área de endemismo aviar # 018, según Stattersfield *et al.*1998), no se ha alcanzado el equilibrio especies-área, y aún con un estado constante del bosque natural, desaparecerán 10 de las 13 especies endémicas observadas en el área de estudio.

En comparación con otras áreas de estudio (para juzgar si el área de estudio, como parte de un hot spot de la biodiversidad a una altura de 2500, se valora o no como rica en especies) en las tierras bajas de Panamá (Robinson *et al.* 2000) o la cuenca del amazonas (Terborgh et al 1990), el área de Chelemhá presenta claras diferencias: la riqueza de especies es reducida y es similar a la avifauna de tierras altas como por ejemplo en Ecuador arriba de 3000 m (Poulson & Krabbe 1997) o a la de tierras bajas templadas norteamericanas (Illinois; Karr 1971). Desde el punto de vista evolutivo, 13 de las 28 familias son elementos neotropicales o sudamericanos, 15 cosmopolitas y norteamericanas.

Debido a que el bosque natural se encuentra mejor que el bosque secundario en cuanto a abundancias, distribución de masas corporales, territorialidad y porción de especies especialistas y endémicas, se valora como esencial la conservación de los fragmentos de bosque natural que quedan en la Sierra Yalijux, ya que solamente así podrán protegerse de la desaparición regional, y a largo plazo, las especies especialistas y endémicas.

Como especies meta pueden tenerse al quetzal (*Pharomachrus mocinno*) y al mono aullador de Yucatán *Alouatta pigra*, ya que por un lado son dependientes directos del estado bosque natural a largo plazo y por otro lado, son marcados en sus hábitos y comportamiento. En el crecimiento secundario (más joven de 10 años), no aparece el mono aullador, y el quetzal solamente si han quedado allí los troncos de árboles muertos que necesita para incubar. Por estas razones, la conservación del bosque natural remanente es imprescindible para conservar a largo plazo a especies como el quetzal.

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Appendix A

Table 18: Observed (Obs) and expected species (Howell & Webb 1995) in the Sierra Yalijux and Chicacnab (CHI; Eisermann 2000 *in lit.*). Net: species captured at the study plot; TC: species recorded by transect census techniques at the study plot; Ex: extinct in Sierra Yalijux extinct referring to locals; 2200: species with upper range at 2200 m referring to Howell & Webb (1995), NE: not expected in the study area referring to Howell & Webb (1995). Systematic order follows American Ornithologists' Union (1998).

Species	Obs	Net	TC	Expected	CHI	Ex	NE	2200
Total: 184	99	64	75	141	136	1	3	7
Ardea herodias					x			
Bubulcus ibis					x			
Coragyps atratus				x	x			
Chondrohierax uncinatus	x		x	x	x			
Elanoides forficatus					x			
Accipiter chinogaster				x	x			
Asturina nitida					x			
Buteo platypterus					x			
Buteo solitarius				x				x
Buteo jamaicensis	x			x	x			
Micrastur ruficollis				x	x			x
Falco sparverius				x	x			
Ortalis vetula	x		x	x	x			
Penelope purpurascens				x				
Penelopina nigra	x		x	x	x			
Oreophasis derbianus				x		x		
Dendrortyx leucophrys	x		x	x	x			
Odontophorus guttatus				x				x
Dactylortyx thoracicus				x				
Cyrtonyx ocellatus	x		x	x				
Bartramia longicauda					x			
Columba livia				x				
Columba fasciata	x		x	x	x			
Zenaida asiatica				x				
Zenaida macroura					x			
Columbina inca				x				
Columbina passerina				x				
Claravis mondetoura	x	x		x				
Leptotila verreauxi					x			
Geotrygon albifacies	x	x		x	x			
Bolborhynchus lineola	x		x	x	x			
Piaya cayana				x				x
Tyto alba				x				
Otus trichopsis				x				
Otus barbarus				x				
Lophostrix cristata	x			x				
Glaucidium gnoma	x			x	x			
Ciccaba virgata	x		x	x	x			
Strix fulvescens	x		x	x	x			
Asio stygius				x				x
Aegolius ridgway				x				
Chordeiles acutipennis				x				
Caprimulgus arizonae	x		x	x	x			
Cypseloides niger	x		x	x	x			
Streptoprocne rutila				x	x			
Streptoprocne zonaris				x	x			
Chaetura vauxi				x	x			
Aeronautes saxatalis	x		x	x	x			
Campylopterus hemileucurus	x	x		x	x			
Colibri thalassinus	x	x	x	x	x			
Abeillia abeillei	x	x	x	x				
Chlorostilbon canivetii	x			x				
Hylocharis leucotis	x	x		x	x			
Amazilia cyanocephala	x	x		x				
Lampornis viridipallens	x	x	x	x	x			
Lampornis amethystinus	x	x	x	x	x			
Lamprolaima rhami	x	x	x	x	x			
Eugenes fulgens	x	x	x	x	x			
Doricha enicura	x	x		x				
Tilmatura dupontii	x		x	x	x			
Atthis ellioti	x	x	x	x	x			
Trogon mexicanus	x		x	x	x			
Trogon collaris	x		x	x				
Pharomachrus mocinno	x	x	x	x	x			
Asphata gularis	x	x	x	x	x			
Aulacorhynchus prasinus	x	x	x	x	x			
Melanerpes formicivorus				x				
Melanerpes aurifrons				x	x			
Sphyrapicus varius					x			
Picoides villosus	x	x	x	x	x			
Piculus rubiginosus				x				x
Colaptes auratus	x	x	x	x	x			
Anabacerthia variegaticeps				x	x			
Automolus rubiginosus	x	x	x	x	x			
Sclerurus mexicanus	x		x	x	x			
Xiphocolaptes promeropirhynchus				x				
Xiphorhynchus erythropygius	x	x	x	x	x			
Lepidocolaptes affinis	x	x	x	x	x			
Grallaria guatimalensis	x	x		x				
Camptostoma imberbe	x	x		x				
Elaenia frantzii					x			
Zimmerius vilissimus	x	x	x	x	x			
Mitrephanes phaeocercus	x		x	x	x			
Cantopus pertinax	x		x	x				
Cantopus sordidulus					x			
Contopus virens					x			
Cantopus cinereus					x			
Contopus borealis					x			
Empidonax flaviventris					x			
Empidonax virescens					x			
Empidonax minimus					x			
Empidonax hammondii					x			
Empidonax oberholseri					x			
Empidonax affinis	x	x		x				
Empidonax flavescens	x	x	x	x	x			
Empidonax fulvifrons				x	x			
Sayornis nigricans				x	x			
Pachyramphus major				x				
Pachyramphus aglaiae				x	x			
Vireo plumbeus	x	x	x	x	x			
Vireo huttoni	x			x	x			
Vireo gilvus					x			
Vireo leucophrys					x			
Vireo philadelphicus					x			
Cyclarhis gujanensis					x			
Cyanocitta stelleri				x				
Cyanocorax melanocyaneus	x	x	x	x	x			
Cyanolyca pumilo	x	x	x	x	x			
Aphelocoma unicolor				x				
Corvus corax	x		x	x				
Tachycineta bicolor				x	x			
Tachycineta thalassina	x		x	x				
Notiochelidon pileata	x		x	x	x			
Petrochelidon pyrrhonota					x			
Hirundo rustica					x			
Certhia americana				x				
Thryothorus modestus	x	x	x	x	x			
Troglodytes musculus	x	x	x	x	x			
Troglodytes rufociliatus	x	x	x	x	x			
Henicorhina leucophrys	x	x	x	x	x			
Sialia sialis				x	x			
Myadestes occidentalis	x	x	x	x	x			
Myadestes unicolor	x	x	x	x	x			
Catharus aurantiirostris	x	x	x	x	x			
Catharus frantzii	x	x	x	x	x			
Catharus mexicanus	x			x				
Catharus dryas				x				
Catharus ustulatus					x			
Catharus guttatus					x			
Turdus infuscatus	x	x	x	x	x			
Turdus plebejus	x	x	x	x	x			
Turdus grayi	x	x	x	x	x			
Turdus rufitorques	x		x	x	x			
Dumetella carolinensis					x			
Melanotis hypoleucus	x	x	x	x	x			
Ptilogonys cinereus				x	x			
Peucedramus taeniatus				x	x			
Vermivora chrysoptera	x	x		x				
Vermivora peregrina					x			
Parula superciliosa	x	x	x	x	x			
Dendroica pensylvanica					x			
Dendroica coronata					x			
Dendroica virens					x			
Dendroica townsendi	x				x		x	
Dendroica occidentalis					x			
Dendroica fusca	x	x	x	x	x			
Dendroica graciae				x				
Mniotilta varia					x			
Seiurus noveboracensis					x			
Seiurus motacilla					x			
Oporornis tolmiei	x	x	x	x	x			
Geothlypis poliocephala	x	x		x	x			
Wilsonia pusilla	x	x	x	x	x			
Wilsonia canadensis					x			
Ergaticus versicolor	x	x		x	x			
Myioborus miniatus	x	x	x	x	x			
Basileuterus rufifrons	x	x		x	x			
Basileuterus belli	x	x	x	x	x			
Chlorospingus ophthalmicus	x	x	x	x	x			
Piranga flava				x				
Euphonia elegantissima	x		x	x	x			
Chlorophonia occipitalis	x		x	x	x			
Volatinia jacarina	x	x			x		x	
Sporophila torqueola	x	x	x	x	x			
Tiarias olivacea	x	x	x	x	x			
Haplospiza rustica	x		x	x				
Diglossa baritula	x	x	x	x	x			
Atlapetes gutteralis	x	x	x	x	x			
Buarremon brunneinucha	x	x	x	x	x			
Melozone biarcuatum	x	x	x	x				
Aimophila rufescens	x	x		x	x			
Spizella passerina	x	x		x				
Zonotrichia capensis	x	x	x	x	x			
Saltator coerulescens					x			
Saltator atriceps	x		x	x				
Pheucticus ludovicianus					x			
Dives dives	x		x	x	x			
Quiscalus mexicanus	x		x	x	x			
Molothrus aeneus				x				
Icterus chrysater				x	x			x
Icterus galbula					x			
Carduelis notata	x	x	x	x	x			
Carduelis atriceps	x	x					x	
Coccothraustes abeillei				x	x			

Table 19: Nutrition guild composition of the bird community in Chelemhá. Separated by technique (mist netting and transect census). Species numbers and individuals are given for the study plot (Total), natural forest (NF), and young secondary forest (YSF) in absolute numbers and percentages.

Mist Netting		Habitat	Insectivore	Nectarivore	Granivore	Frugivore	Omnivore	Carnivore
Absolute	Individuals	Total	157	336	74	2	267	0
		NF	63	158	8	1	137	0
		YSF	94	178	66	1	150	0
	Species	Total	25	12	11	2	10	0
		NF	11	7	2	1	9	0
		YSF	20	12	11	1	7	0
Percentage	Individuals	Total	0.188	0.402	0.089	0.002	0.319	0.000
		NF	0.172	0.431	0.022	0.003	0.373	0.000
		YSF	0.192	0.364	0.135	0.002	0.307	0.000
	Species	Total	0.417	0.200	0.183	0.033	0.167	0.000
		NF	0.367	0.233	0.067	0.033	0.300	0.000
		YSF	0.392	0.235	0.216	0.020	0.137	0.000
Transect Census		Habitat	Insectivore	Nectarivore	Granivore	Frugivore	Omnivore	Carnivore
Absolute	Individuals	Total	467	149	172	90	597	2
		NF	288	95	71	53	432	2
		YSF	179	55	100	37	158	2
	Species	Total	31	9	12	7	14	3
		NF	26	6	5	7	10	2
		YSF	58	20	27	14	41	4
Percentage	Individuals	Total	0.316	0.101	0.116	0.061	0.404	0.001
		NF	0.306	0.101	0.076	0.056	0.459	0.002
		YSF	0.337	0.103	0.189	0.070	0.298	0.003
	Species	Total	0.408	0.118	0.158	0.092	0.184	0.039
		NF	0.464	0.107	0.089	0.125	0.179	0.036
		YSF	0.355	0.122	0.165	0.086	0.251	0.021

Table 20: Dissimilarity matrix of Sørensen-Index. Letters represent net lines in the study plot of the Sierra Yalijux ([a] to [k]: natural forest, [m] to [r]: young secondary forest). Sørensen is measured with six repetitions at each net line.

	[a]	[b]	[c]	[e]	[l]	[k]	[m]	[n]	[o]	[p]	[q]	[r]
[a]	0.00											
[b]	0.33	0.00										
[c]	0.23	0.44	0.00									
[e]	0.35	0.35	0.46	0.00								
[i]	0.42	0.43	0.35	0.33	0.00							
[k]	0.26	0.19	0.32	0.55	0.33	0.00						
[m]	0.43	0.57	0.50	0.57	0.55	0.46	0.00					
[n]	0.29	0.38	0.38	0.52	0.57	0.37	0.45	0.00				
[o]	0.36	0.50	0.40	0.50	0.52	0.43	0.43	0.32	0.00			
[p]	0.43	0.52	0.46	0.58	0.50	0.46	0.45	0.46	0.28	0.00		
[q]	0.46	0.51	0.49	0.59	0.58	0.49	0.48	0.44	0.29	0.29	0.00	
[r]	0.35	0.42	0.41	0.50	0.59	0.45	0.53	0.30	0.38	0.41	0.35	0.00

Table 21: Dissimilarity matrix of Sørensen-Index of understory birds in the study plot of the Sierra Yalijux. Letters represent net lines in the study plot of the Sierra Yalijux ([a] to [k]: natural forest, [m] to [r]: young secondary forest). Sørensen is measured with six repetitions at each net line.

	[a]	[b]	[c]	[e]	[l]	[k]	[m]	[n]	[o]	[p]	[q]	[r]
[a]	0.00											
[b]	0.33	0.00										
[c]	0.17	0.33	0.00									
[e]	0.17	0.33	0.17	0.00								
[i]	0.56	0.56	0.56	0.56	0.00							
[k]	0.27	0.27	0.27	0.27	0.25	0.00						
[m]	0.37	0.50	0.37	0.50	0.69	0.60	0.00					
[n]	0.20	0.33	0.20	0.33	0.67	0.43	0.16	0.00				
[o]	0.47	0.47	0.33	0.47	0.67	0.57	0.16	0.33	0.00			
[p]	0.37	0.25	0.25	0.37	0.54	0.33	0.20	0.26	0.16	0.00		
[q]	0.37	0.25	0.25	0.37	0.54	0.33	0.30	0.26	0.16	0.10	0.00	
[r]	0.50	0.50	0.33	0.50	0.78	0.64	0.37	0.33	0.33	0.25	0.25	0.00

Table 22: Dissimilarity matrix of Morisita-Horn-Index of understory birds in the study plot of the Sierra Yalijux. Letters represent net lines in the study plot of the Sierra Yalijux ([a] to [k]: natural forest, [m] to [r]: young secondary forest). Morisita-Horn is measured with six repetitions at each net line.

	[a]	[b]	[c]	[e]	[I]	[k]	[m]	[n]	[o]	[p]	[q]	[r]
[a]	0.00											
[b]	0.19	0.00										
[c]	0.03	0.13	0.00									
[e]	0.22	0.09	0.15	0.00								
[i]	0.48	0.45	0.40	0.36	0.00							
[k]	0.33	0.22	0.30	0.27	0.57	0.00						
[m]	0.67	0.60	0.61	0.61	0.76	0.82	0.00					
[n]	0.36	0.18	0.31	0.19	0.38	0.55	0.41	0.00				
[o]	0.75	0.73	0.76	0.76	0.86	0.77	0.19	0.56	0.00			
[p]	0.72	0.82	0.74	0.82	0.80	0.59	0.38	0.80	0.15	0.00		
[q]	0.69	0.85	0.80	0.84	0.81	0.63	0.61	0.81	0.27	0.23	0.00	
[r]	0.76	0.80	0.84	0.84	0.85	0.67	0.61	0.71	0.21	0.23	0.10	0.00

Table 23: Vegetation structure in Chelemhá (OTS: overstory tree size (cm), OTD overstory tree density (cm), OTH overstory tree height (m), UTD: understory tree density (cm), UTS: understory tree size (cm), UTH: understory tree height (m); TC: point of transect census or mist net were vegetation was recorded, Forest indicates forest type, NF: natural forest, YSF: young secondary forest, SF: secondary forest. Numbers in brackets indicate second data set which is not included into analysis.

TC	Forest	Levey	OTS	OTH	OTD	UTS	UTH	UTD	TC	Forest	Levey	OTS	OTH	OTD	UTS	UTH	UTD
a1	NF	s3	60	20	250	3	4	100	i2	NF	s3	50	25	90	7	5	110
a2	NF	s3	90	30	300	10	4	80	i3	NF	s3	60	25	90	5	5	250
a3	NF	s3	30	20	300	2	5	200	i4	NF	s3	70	25	250	1	2	190
a4	NF	g	-	-	-	6	7	150	i5	NF	s3	60	15	200	8	7	110
a5	NF	s3	30	25	150	9	5	100	i6b	NF	s3	(130)	(30)	(250)	3	3	190
a6	NF	s3	50	30	400	5	7	100	i6	NF	s3	60	15	70	3	3	190
a7	NF	s3	50	30	400	5	7	100	i6	NF	s3	130	30	250	3	3	190
a8b	NF	g	-	-	-	3	9	200	i7	NF	s3	20	15	150	7	4	150
a8	NF	g	200	35	800	3	9	200	i8	NF	s3	60	15	90	1	2	50
b1	NF	s3	30	15	200	2	4	180	k1	NF	s3	100	25	250	2	2	130
b2	NF	s3	40	20	600	10	7	60	k2	NF	s3	50	25	120	5	4	120
b3	NF	s3	40	15	430	1.5	2	80	k3	NF	s3	40	25	400	2	5	160
b4	NF	s3	60	20	130	3	3	200	k4	NF	s3	70	25	180	7	6	60
b5	NF	s3	120	25	300	3	4	210	k5	NF	s3	40	25	360	5	5	190
b6	NF	s3	50	15	80	3	4	40	k6	NF	s3	150	25	280	7	5	280
b7	NF	s3	110	25	190	2	3	170	k7	NF	s3	100	25	130	6	7	80
b8b	NF	s3	>200	30	170	4	4	130	k8	NF	s3	120	25	600	2	3	120
b8	NF	s3	200	30	170	4	4	130	m1	YSF	s1	-	-	-	1	2	200
c1	NF	s3	40	25	210	10	7	170	m2	YSF	s1	-	-	-	7	7	170
c2	NF	g	50	20	480	7	5	150	m3	YSF	s1	-	-	-	2	4	100
c3	NF	s3	20	15	190	7	6	200	m4	YSF	s1	-	-	-	4	4	100
c4	NF	s3	15	10	190	5	4	110	m5	YSF	s1	-	-	-	3	5	30
c5	NF	s3	30	20	290	1.5	2	70	m6	YSF	s1	-	-	-	1	4	20
c6	NF	s3	30	15	270	2	2.5	190	m7	YSF	s1	-	-	-	1	4	20
c7b	NF	s3	180	20*	140	2	2.5	160	m8	YSF	s1	-	-	-	1	4	20
c7	NF	s3	180	20	140	2	2.5	160	n1	YSF	s1	-	-	-	4	3	100
c8	NF	s3	40	25	280	2.5	3	130	n2	SF	s1	-	-	-	4	3	130
d1	NF	s3	90	30	300	10	4	80	n3b	SF	s2	(40)	(15)	(130)	5	5	190
d2	NF	s3	40	25	350	2	3	100	n3	SF	s2	40	15	130	5	5	190
d3	NF	g	-	-	-	6	7	150	n4b	SF	s2	(20)	(10)	(200)	4	8	140
d4	NF	s3	220	35	200	3	4	130	n4	SF	s2	20	10	200	4	8	140
d5	NF	s3	50	30	150	6	5	150	n5	SF	s2	-	-	-	8	6	100
d6	NF	s3	40	20	600	10	7	60	n6	SF	s1	25	10	600	4	5	0
d7	NF	s3	30	15	200	2	4	180	n7	SF	s1	210	10	140	6	5	120
d8	NF	s3	50	30	150	3	4	150	n8	SF	s2	-	-	-	4	6	100
d9	NF	s3	200	25	300	7	4	100	o1	YSF	s1	-	-	-	1	0.5	200
d10	NF	s3	50	30	250	3	5	100	o2	YSF	s1	-	-	-	2	3	50
d11	NF	s3	160	25	300	5	4	150	o3	YSF	s1	-	-	-	2	4	50
d12	NF	s3	40	25	100	3	6	10	o4	YSF	s1	-	-	-	2	3	50
d13	NF	s3	25	25	150	7	7	150	o5	YSF	s1	-	-	-	2	3	50
d14	NF	s3	25	25	150	7	7	150	o6	YSF	s1	-	-	-	2	3	50
e1	NF	s3	160	30	230	5	7	230	o7	YSF	s1	-	-	-	2	3	50
e2	NF	s3	40	15	310	3	5	90	o8	YSF	s1	-	-	-	2	3	50
e3	NF	s3	50	25	300	5	6	220	p1	YSF	s1	-	-	-	1	0.5	200
e4b	NF	s3	80	30	30	5	4	200	p2	YSF	s1	-	-	-	1	0.5	200
e4c	NF	s3	80	30	30	15	8	300	p3	YSF	s1	-	-	-	1	0.5	200
e4	NF	s3	80	30	30	5	4	200	p4	YSF	s1	-	-	-	1	0.5	200
e5	NF	s3	90	30	200	5	7	80	p5	YSF	s1	-	-	-	1	0.5	200
e6	NF	s3	25	20	90	5	5	90	p6	YSF	s1	-	-	-	1	0.5	200
e7	NF	s3	20	15	110	1	6	150	p7	YSF	s1	-	-	-	1	0.5	200
e8	NF	s3	120	30	250	1	6	130	p8	YSF	s1	-	-	-	1	0.5	200
f1	NF	g	50	20	480	7	5	150	q1	YSF	s1	-	-	-	1	0.5	200
f2	NF	g	50	20	480	7	5	150	q2	YSF	s1	-	-	-	1	0.5	200

TC	Forest	Levey	OTS	OTH	OTD	UTS	UTH	UTD
f3	NF	s3	250	35	250	3	3	250
f4	NF	s3	60	25	250	9	6	200
f5	NF	s3	100	35	350	2	2	50
f6	NF	s3	130	30	100	10	7	100
f7	NF	s3	120	35	250	10	8	160
f8	NF	s3	100	35	210	8	10	300
f9	NF	s3	110	30	250	6	5	200
f10	NF	s3	130	35	350	7	5	150
f11	NF	s3	50	35	300	5	3	150
f12	NF	s3	140	20	500	2	4	100
f13	NF	s3	40	35	400	4	4	300
f14	NF	s3	90	35	150	2	5	100
f15	NF	s3	130	35	400	3	4	100
f16	NF	s3	200	35	700	6	9	150
f17	NF	s3	40	35	250	10	10	150
f18	NF	s3	30	30	120	4	3.5	200
f19	NF	s3	120	35	150	8	8	200
f20	NF	s3	100	35	250	5	6	250
f21	NF	s3	100	35	300	9	8	150
f22	NF	s3	140	30	500	4	7	300
f23	NF	s3	100	35	400	6	9	400
f24	NF	s3	200	35	500	10	7	250
f25*	NF	g	-90	-30	-300	7	6	200
f25	NF	g	90	30	300	7	6	200
f26*	NF	g	-200	-35	-800	4	4	50
f26	NF	g	200	35	800	4	4	50
f27	NF	s3	25	30	350	2	3	250
f28	NF	s3	30	30	500	6	6	100
f29	NF	s3	150	35	200	7	8	200
f30	NF	s3	110	35	150	4	4	300
f31	NF	s3	130	30	400	9	7	120
f32	NF	s3	120	30	350	10	6	150
f33	NF	s3	40	30	500	6	5	150
f34	NF	s3	80	35	200	9	2.5	200
f35	NF	s3	70	35	300	7	4	300
f36	NF	s3	70	25	250	1	2	190
g1b	NF	s3	120	25	600	2	3	120
g1	NF	s3	100	30	350	5	6	200
g2b	NF	s3	40	25	360	5	5	190
g2	NF	s3	150	35	150	7	6	250
g3	NF	s3	40	30	250	10	3	250
g4	NF	s3	150	30	700	4	4	300
g5	NF	s3	80	35	300	6	6	150
g6	NF	s3	50	30	700	3	3	300
g7	NF	s3	120	25	800	4	5	100
g8	NF	s3	60	25	200	3	6	200
g9	NF	s3	150	30	400	2	4	80
g10	NF	s3	90	25	300	9	6	50
g11	NF	s3	80	25	300	2	4	100
g12	NF	s3	90	30	400	2	3	100
g13	NF	s3	150	30	500	8	6	250
g17	NF	s3	25	25	350	8	6	100
g18	NF	s3	35	25	250	4	4	100
g19b	NF	g	(15)	(10)	(300)	5	4	900
g19	NF	g	15	10	300	5	4	900
i1	NF	s3	40	20	170	4	5	150
q3	YSF	s1	-	-	-	1	0.5	200
q4	YSF	s1	-	-	-	1	0.5	200
q5	YSF	s1	-	-	-	1	0.5	200
q6	YSF	s1	-	-	-	1	0.5	200
q7	YSF	s1	-	-	-	1	0.5	200
q8	YSF	s1	-	-	-	1	0.5	200
r1	YSF	s1	-	-	-	1	0.5	200
r2	YSF	s1	-	-	-	1	0.5	200
r3	YSF	s1	-	-	-	1	0.5	200
r4	YSF	s1	-	-	-	1	0.5	200
r5	YSF	s1	-	-	-	1	0.5	200
r6	YSF	s1	-	-	-	1	0.5	200
r7	YSF	s1	-	-	-	1	0.5	200
r8	YSF	s1	-	-	-	1	0.5	200
t1	YSF	s1	-	-	-	2	3	20
t2	YSF	s1	-	-	-	2	3	20
t3	YSF	s1	-	-	-	2	3	20
t4	YSF	s1	-	-	-	2	3	20
t5	YSF	s1	-	-	-	2	3	20
t6	YSF	s1	-	-	-	2	3	20
t7	YSF	s1	-	-	-	2	3	20
u7	NF	s1	60	20	550	4	5	240
u8	NF	g	-	-	-	-	-	-
u9	NF	s3	60	25	130	10	8	240
u10	NF	s3	170	20	340	4	6	220
u11	NF	s3	-	-	-	3	3	100
u12	NF	s3	50	25	60	7	4.5	120
u13	NF	s3	50	25	60	7	4.5	120
w1	YSF	s1	-	-	-	2	3	20
w2	YSF	s1	-	-	-	2	3	20
w3	YSF	s1	-	-	-	2	3	20
w4	YSF	s1	-	-	-	2	3	20
w5	YSF	s1	-	-	-	2	3	20
w6	YSF	s1	-	-	-	2	3	20
w7	YSF	s1	-	-	-	2	3	20
w8	YSF	s1	-	-	-	2	3	20
w9	YSF	s1	-	-	-	2	3	20
x1	YSF	s1	-	-	-	2	3	20
x2	NF	s3	50	20	250	5	4	20
x3	NF	s3	50	20	250	5	4	270
x4	NF	s3	90	25	1000	6	4	120
x5	NF	s3	160	25	100	10	9	350
x6	NF	s3	60	25	150	3	3	100
x7	NF	g	-	-	-	-	-	-
x8	NF	s3	30	15	300	2	2	50
x9	NF	s3	120	15	200	-	-	-
x10	NF	g	40	20	300	-	-	-
x11	NF	g	30	20	300	-	-	-
x12	NF	s3	120	25	300	-	-	-
x13	NF	s3	-	-	-	1	1	30
x14	NF	s3	-	-	-	1	1	30
x15	NF	s3	-	-	-	1	1	30
x16	NF	s3	25	20	170	6	6	100
x17	NF	s3	90	20	400	7	6	60
x18	NF	s3	30	15	50	7	8	100
x19	NF	g	(80)	(25)	(350)	8	7	100

Table 24: Results log series, lognormal, and broken stick species distribution models (Magurran 1988). Boundary: upper boundary of class; S: Species number; N: individuals; σ²: variance of lognormal; x: mean of lognormal distribution; Se: estimated species number, NF: natural forest; YSF; young secondary forest; TOTAL: study plot. GOF: χ² goodness of fit test.

LOGSERIES:					LOGNORM:							BROKEN STICK:				
TOTAL	Class	Boundary	Expected	Observed	TOTAL	Class	Boundary	Expected	Observed			TOTAL	Class	Boundary	Expected	Observed
	1	1.5	7.89	19		1	1.5	14.53	20	S=	64		1	1.5	3.67	14
	2	3.5	6.38	20		2	3.5	11.28	6	N=	1036		2	3.5	6.70	18
	3	7.5	5.47	6		3	7.5	8.16	3				3	7.5	11.22	9
	4	15.5	4.61	3		4	15.5	5.4	10	x=	0.298		4	15.5	15.73	4
	5	31.5	3.52	10		5	31.5	3.23	4	σ²=	0.786		5	31.5	15.61	7
	6	63.5	2.14	4		6	63.5	1.73	1	Se=	85		6	63.5	7.96	2
	7	127.5	0.83	1		7	127.5	0.83	1				7	127.5	1.17	1
	8	255.5	0.14	1		8	255.5	0.36	0				8	255.5	0.02	0
	9	511.5	0.00	0		9	511.5	0.14	0				9	511.5	0.00	0
GOF: p =				6.71x10-11					0.121							2.32x10-11
YSF	1	1.5	15.32	14		1	1.5	14.25	14	S=	55		1	1.5	5.37	20
	2	3.5	12.22	18		2	3.5	13.99	18	N=	497		2	3.5	9.16	6
	3	7.5	10.19	9		3	7.5	11.39	9				3	7.5	13.35	3
	4	15.5	8.14	4		4	15.5	7.76	4	x=	0.403		4	15.5	14.25	10
	5	31.5	5.59	7		5	31.5	4.4	7	σ²=	0.442		5	31.5	8.33	4
	6	63.5	2.76	2		6	63.5	2.07	2	Se=	64		6	63.5	1.57	1
	7	127.5	0.73	1		7	127.5	0.8	1				7	127.5	0.03	1
	8	255.5	0.06	0		8	255.5	0.25	0				8	255.5	0.00	0
	9	511.5	0.00	0		9	511.5	0.07	0				9	511.5	0.00	0
GOF: p =				0.666					0.715							5.00x10-14
NF	1	1.5	2.05	8		1	1.5	6.8	8	S=	30		1	1.5	2.34	8
	2	3.5	1.66	2		2	3.5	5.49	2	N=	367		2	3.5	4.15	2
	3	7.5	1.42	3		3	7.5	4.05	3				3	7.5	6.56	3
	4	15.5	1.20	4		4	15.5	2.68	4	x=	0.312		4	15.5	8.19	4
	5	31.5	0.92	3		5	31.5	1.58	3	σ²=	0.696		5	31.5	6.41	3
	6	63.5	0.56	1		6	63.5	0.83	1	Se=	39		6	63.5	2.01	1
	7	127.5	0.22	0		7	127.5	0.38	0				7	127.5	0.11	0
	8	255.5	0.04	0		8	255.5	0.16	0				8	255.5	0.00	0
	9	511.5	0.00	0		9	511.5	0.06	0				9	511.5	0.00	0
GOF: p =				0.0001					0.729							0.006

Table 25: Vertical stratification classes of all captured birds. Observations made during transect census. 2: frequent observations, 1: medium observations, 0: no observations, x: presumably present in this class but neither records nor literature based proof.

Species	< 7 m	7 - 20 m	> 20 m
Chlorospingus ophthalmicus	1	1	1
Lampornis amethystinus	1	1	1
Catharus frantzii	1	2	0
Lamprolaima rhami	1	1	1
Diglossa baritula	2	0	0
Basileuterus belli	2	1	0
Buarremon brunneinucha	2	0	0
Henicorhina leucophrys	2	0	0
Atlapetes gutteralis	2	0	0
Colibri thalassinus	2	1	0
Hylocharis leucotis	1	x	0
Wilsonia pusilla	1	1	0
Myadestes occidentalis	1	2	1
Turdus infuscatus	2	1	0
Lampornis viridipallens	1	1	1
Empidonax flavescens	1	1	0
Myadestes unicolor	0	2	x
Turdus plebejus	1	2	0
Eugenes fulgens	1	1	0
Troglodytes musculus	2	0	0
Troglodytes ruficiliatus	2	0	0
Catharus aurantiirostris	2	1	0
Empidonax affinis	1	1	1
Amazilia cyanocephala	1	1	1
Asphata gularis	2	1	0
Tiarias olivacea	1	x	x
Basileuterus rufifrons	2	1	0
Myioborus miniatus	2	0	0
Oporornis tolmiei	1	x	x
Thryothorus modestus	2	0	0
Turdus grayi	1	1	1
Abeillia abeillei	1	x	x
Automolus rubiginosus	1	0	0
Campylopterus hemileucurus	1	1	1
Colaptes auratus	0	1	1
Cyanolyca pumilo	0	1	1
Melanotis hypoleucus	1	1	0
Picoides villosus	x	1	1
Atthis ellioti			
Carduelis atriceps	1	1	x
Carduelis notata	1	1	x
Melozone biarcuatum	2	0	0
Spizella passerina			
Sporophila torqueola	1	0	0
Parula superciliosa			
Vireo plumbeus			
Volatinia jacarina			
Xiphorhynchus erythropygius	0	1	1
Zonotrichia capensis	2	0	0
Aimophila rufescens			
Aulacorhynchus prasinus	0	1	1
Camptostoma imberbe			
Claravis mondetoura	1	0	0
Cyanocorax melanocyaneus	1	1	1
Dendroica fusca			
Doricha enicura			
Ergaticus versicolor			
Geothlypis poliocephala			
Geotrygon albifacies			
Grallaria guatimalensis	2	0	0
Lepidocolaptes affinis	0	1	1
Pharomachrus mocinno	0	1	2
Vermivora chrysoptera			
Zimmerius vilissimus	0	1	2

Table 26: Captures (C), recaptures (R) and recapture rate (R^t) listed per habitat for the Sierra Yalijux. NF: natural forest, YSF: young secondary forest. Sorted by captures.

	C				R			R in:			R^t			C/R
Species	Total	NF	YSF	Total	NF	YSF	Both	NF	YSF	Total	NF	YSF	NF	YSF
Chlorospingus ophthalmicus	148	57	91	23	9	14	1			0.155	0.16	0.15	6.333	6.500
Lampornis amethystinus	126	76	50	7	6	1	1			0.056	0.08	0.02	12.667	50.000
Catharus frantzii	63	41	22	35	29	6	1			0.556	0.71	0.27	1.414	3.667
Lamprolaima rhami	62	52	10	12	12	0			1	0.194	0.23	0.00	4.333	
Diglossa baritula (e)	45	8	37	21	0	21		1		0.467	0.00	0.57		1.762
Basileuterus belli	39	24	15	19	11	8	1			0.487	0.46	0.53	2.182	1.875
Buarremon brunneinucha	31	6	25	7	1	6	1			0.226	0.17	0.24	6.000	4.167
Henicorhina leucophrys	28	19	9	12	10	2	1			0.429	0.53	0.22	1.900	4.500
Wilsonia pusilla	25	1	24	5	0	5		1		0.200	0.00	0.21		4.800
Atlapetes gutteralis	23	2	21	8	0	8		1		0.348	0.00	0.38		2.625
Myadestes occidentalis	22	1	21	4	1	3	1			0.182	1.00	0.14	1.000	7.000
Lampornis viridipallens	20	16	4	1	1	0			1	0.050	0.06	0.00	16.000	
Empidonax flavescens (e)	18	10	8	2	2	0			1	0.111	0.20	0.00	5.000	
Myadestes unicolor	13	8	5	1	1	0			1	0.077	0.13	0.00	8.000	
Troglodytes musculus	6	0	6	1	0	1		1		0.167		0.17		6.000
Troglodytes ruficiliatus	6	3	3	1	0	1		1		0.167	0.00	0.33		3.000
Asphata gularis (e)	5	1	4	2	0	2		1		0.400	0.00	0.50		2.000
Basileuterus rufifrons	3	0	3	1	0	1		1		0.333		0.33		3.000
Oporornis tolmiei	3	0	3	1	0	1		1		0.333		0.33		3.000
Catharus aurantiirostris	2	2	0	1	1	0			1	0.500	0.50		2.000	
Melanotis hypoleucus (e)	2	0	2	1	0	1		1		0.500		0.50		2.000
Myioborus miniatus	2	0	2	2	0	2		1		1.000		1.00		1.000
Thryothorus modestus	2	0	2	2	0	2		1		1.000		1.00		1.000
Abeillia abeillei (e)	1	0	1	1	0	1		1		1.000		1.00		1.000
Xiphorhynchus erythropygius	1	1	0	1	1	0			1	1.000	1.00		1.000	
Total	696	328	368	171	85	86								
Numbers														
R in one Habitat								12	6					
R in both Habitats							7							
Medium Rt										0.397	0.290	0.344		

Table 27: Multiple regression number individuals versus vegetation structure parameters in Chelemhá for selected species. SD: standard deviation, OTD: overstory tree density, OTH: overstory tree height, UTD: understory tree density, UTH: understory tree height, r² corr: corrected r².

	ß	SD ß	B	SD B	t(2)	p-level
Diglossa baritula						
r = 0.87	r² = 0.76	r² corr = -				
F(4,1) = 0.81	p < 0.67149					
Const.			-11.20	12.48	-0.89	0.53
OTD	1.81	1.41	1.82	1.42	1.287	0.42
OTH	-1.04	1.49	-0.15	0.22	-0.70	0.61
UTD	1.43	1.69	7.38	8.65	0.85	0.55
UTH	0.20	0.59	0.17	0.49	0.34	0.78
Basileuterus belli						
r = 0.95,	r² = 0.90	r² corr = 0.72				
F(4,2) = 5.0521	p < 0.17					
Const.			-10.99	22.58	-0.49	0.67
OTD	0.41	0.49	2.57	3.08	0.84	0.49
OTH	-1.39	0.47	-1.26	0.42	-2.97	0.10
UTD	0.63	0.54	19.28	16.42	1.17	0.36
UTH	0.50	0.23	2.35	1.10	2.156	0.16
Buarremon brunneinucha						
r = 0.97	r² = 0.95	r² corr = 0.85				
F(4,2) = 9.37	p < 0.099					
Const.			23.48	15.08	1.56	0.26
OTD	-0.40	0.37	-2.25	2.06	-1.09	0.39
OTH	-0.593	0.35	-0.4791	0.28	-1.69	0.23
UTD	-0.45	0.40	-12.22	10.97	-1.11	0.38
UTH	0.62	0.17	2.59	0.73	3.56	0.07
Henicorhina leucophrys						
r = 0.79	r² = 0.62	r² corr = -				
F(4,1) = 0.41	p < 0.81					
Const.			-49.4238	48.34	-1.02	0.49
OTD	1.64	1.31	8.55	6.82	1.25	0.43
OTH	-1.62	1.39	-1.04	0.89	-1.17	0.45
UTD	1.74	1.51	39.34	34.13	1.15	0.45
UTH	-0.01	0.65	-0.045	2.31	-0.02	0.99

	ß	SD ß	B	SD B	t(2)	p-level
Atlapetes gutteralis						
r = 0.70	r^2 = 0.49	r^2 corr = 0.24				
F(2,4) = 1.95	p < 0.26					
Const.			16.32	6.12	2.67	0.06
UTD	-1.04	0.54	-5.70	2.95	-1.93	0.13
UTH	-0.93	0.54	-1.41	0.82	-1.72	0.16
Colibri thalassinus						
r = 0.31	r^2 = 0.10	r^2 corr = -				
F(2,4) = 0.22	p < 0.81					
Const.			3.48	6.48	0.54	0.62
UTD	0.22	0.76	0.90	3.14	0.27	0.79
UTH	-0.12	0.76	-0.13	0.87	-0.15	0.89
Hylocharis leucotis						
r = 0.17	r^2 = 0.03	r^2 corr = -				
F(2,2) = 0.031	p < 0.96987					
Const.			-0.15	25.69	-0.01	0.99
UTD	0.48	1.93	2.97	11.92	0.25	0.82
UTH	0.46	1.93	1.11	4.69	0.25	0.84
Turdus infuscatus						
r = 0.67	r^2 = 0.45	r^2 corr = 0.27				
F(2,6) = 2.46	p < 0.17					
Const.			0.71	5.48	0.13	0.91
UTD	0.04	0.57	0.18	2.70	0.07	0.95
UTH	0.70	0.57	0.45	0.36	1.24	0.26

Table 28: Multiple regression number of bird species per net line versus vegetation structure parameters. Further explanations see Table 27.

r = 0.92	r^2 = 0.85	r^2 corr = 0.56				
F(4,2) = 2.91	p < 0.27					
	β	SD β	B	SD B	t(2)	p-level
Const.			-12.68	22.61	-0.56	0.63
OTD	1.21	0.63	5.96	3.08	1.94	0.19
OTH	-1.56	0.60	-1.11	0.425	-2.61	0.12
UTD	0.96	0.69	22.99	16.44	1.40	0.30
UTH	0.29	0.29	1.10	1.09	1.00	0.42

Table 29: Morphometrics of birds in natural forest and young secondary forest in the study plot of Chelemhá. NF: natural forest, YSF: young secondary forest, S: sex, BL: bill length, BW: bill width, BH: bill height, T^i: innermost rectrix, T^o: outermost rectrix: G: total length, T: Tarsus (all measurements in mm).

Habitat	S	Species	BL	BW	BH	W	T^i	T^o	G	T
NF		*Amazilia cyanocephala*	23.2	3.85	2.55	59.00	32.00	31.00	100.50	
YSF		*Amazilia cyanocephala*	22.3	3.15	2.50	60.00	29.35	35.10	95.00	
NF		*Atlapetes gutteralis*	11.8	6.60	7.35	72.00	76.00	70.00	170.50	32.10
YSF		*Atlapetes gutteralis*	13.3	6.92	7.86	73.81	77.05	71.20	175.76	31.52
NF		*Basileuterus belli*	10.3	4.09	3.45	58.95	49.86	46.05	119.81	23.99
YSF		*Basileuterus belli*	9.1	3.97	3.31	60.04	51.40	48.45	121.00	24.19
NF		*Buarremon brunneinucha*	12.7	6.36	7.36	82.40	78.50	66.90	190.40	33.40
YSF		*Buarremon brunneinucha*	15.8	6.01	7.07	82.71	79.54	66.93	191.62	33.86
NF		*Catharus frantzii*	14.7	5.19	4.26	85.71	63.88	62.88	163.88	37.95
YSF		*Catharus frantzii*	14.9	4.72	4.29	82.24	64.33	61.70	163.37	37.17
NF		*Chlorospingus ophthalmicus*	10.4	5.03	5.26	70.84	55.52	55.81	136.51	24.77
YSF		*Chlorospingus ophthalmicus*	10.7	5.01	5.32	70.56	55.75	55.82	137.38	24.91
NF		*Colibri thalassinus*	22.8	4.65	2.80	74.50	39.00	42.50	112.50	
YSF		*Colibri thalassinus*	22.6	3.75	2.25	64.41	36.38	38.07	102.95	
NF	f	*Diglossa baritula*	9.8	2.68	3.72	55.10	40.00	40.97	103.40	20.47
YSF	f	*Diglossa baritula*	10.4	2.93	4.18	54.64	39.00	39.00	103.45	19.71
NF	m	*Diglossa baritula*	9.0	2.00	4.00	57.00	42.00	44.50	109.00	20.00
YSF	m	*Diglossa baritula*	10.4	2.89	4.09	56.06	40.17	41.33	108.83	19.76
NF		*Empidonax flavescens*	9.3	5.87	3.38	63.38	52.98	57.20	125.40	19.53
YSF		*Empidonax flavescens*	10.1	5.49	3.48	66.14	54.46	54.11	129.14	18.84
NF	f	*Eugenes fulgens*	35.6	3.95	2.30	72.25	37.50	40.50	122.50	
YSF	f	*Eugenes fulgens*	35.2	3.86	2.76	70.50	37.98	39.50	122.80	
NF		*Henicorhina leucophrys*	13.0	3.85	3.32	54.47	28.04	24.89	104.40	27.25
YSF		*Henicorhina leucophrys*	14.4	3.69	3.45	54.57	27.65	23.33	104.86	26.41
NF	f	*Lampornis amethystinus*	25.2	3.91	2.24	61.38	33.84	36.17	104.33	
YSF	f	*Lampornis amethystinus*	25.1	3.85	2.42	62.60	33.54	34.65	103.30	
NF	m	*Lampornis amethystinus*	24.5	3.49	2.22	64.75	35.39	37.05	105.11	
YSF	m	*Lampornis amethystinus*	24.7	3.42	2.41	63.37	35.37	37.87	107.04	
NF	f	*Lampornis viridipallens*	20.4	2.87	2.11	61.40	32.73	34.89	100.64	
YSF	f	*Lampornis viridipallens*	22.9	3.05	2.30	59.50	31.80	36.30	100.50	
NF	f	*Lamprolaima rhami*	19.7	3.36	2.18	67.41	35.41	39.80	102.37	
YSF	f	*Lamprolaima rhami*	19.0	3.37	2.25	69.00	36.33	37.30	105.00	
NF	m	*Lamprolaima rhami*	20.2	3.39	2.19	73.43	39.13	45.70	109.55	
YSF	m	*Lamprolaima rhami*	20.4	3.00	2.31	73.67	37.93	44.50	108.57	

Habitat	S	Species	BL	BW	BH	W	T^i	T^o	G	T
NF		*Myadestes unicolor*	12.4	7.63	4.40	97.63	81.90	78.63	190.88	23.63
YSF		*Myadestes unicolor*	11.3	6.68	4.14	96.40	81.20	79.00	200.60	23.36
NF		*Troglodytes ruficiliatus*	9.9	3.10	3.00	49.00	32.07	25.67	100.33	20.60
YSF		*Troglodytes ruficiliatus*	17.2	3.73	3.27	50.67	34.50	32.00	105.33	22.20
NF	f	*Turdus infuscatus*	14.7	5.65	6.85	123.00	82.50	87.00	215.00	34.60
YSF	f	*Turdus infuscatus*	14.4	5.50	6.20	120.00	85.00	83.50	217.50	33.60
NF	m	*Turdus infuscatus*	16.5	7.75	6.74	125.11	83.33	86.93	222.44	34.51
YSF	m	*Turdus infuscatus*	15.3	6.50	6.75	129.00	89.00	96.50	219.00	34.25
NF		*Turdus plebejus*	17.7	6.76	7.08	96.78	86.60	101.20	228.80	37.94
YSF		*Turdus plebejus*	23.2	7.52	6.86	130.40	93.60	92.40	230.00	36.73

Table 30: Captured and recaptured species in the study plot of Chelemhá. C: all captures, FC: first captures, R: recaptures, NF: captures in natural forest, YSF: captures in young secondary forest, D_i: dominance.

Species	Captures						Individuals per Net Line											
	C	FC	R	NF	YSF	D_i	[a]	[b]	[c]	[e]	[i]	[k]	[m]	[n]	[o]	[p]	[q]	[r]
Claravis mondetoura	1	1	0	0	1	0.0012	0	0	0	0	0	0	1	0	0	0	0	0
Geotrygon albifacies	1	1	0	0	1	0.0012	0	0	0	0	0	0	0	1	0	0	0	0
Campylopterus hemileucurus	3	3	0	0	3	0.0035	0	0	0	0	0	0	0	2	1	0	0	0
Colibri thalassinus	36	31	0	2	29	0.0358	0	2	0	0	0	0	2	6	5	2	7	7
Abeillia abeillei	3	1	1	0	1	0.0012	0	0	0	0	0	0	0	0	0	1	1	0
Hylocharis leucotis	35	31	0	0	31	0.0358	0	0	0	0	0	0	7	0	5	4	13	2
Amazilia cyanocephala	7	5	0	2	3	0.0058	0	1	0	1	0	0	1	0	1	0	1	0
Lampornis viridipallens	25	20	1	16	4	0.0231	5	7	4	0	0	1	0	1	0	1	2	0
Lampornis amethystinus	163	126	7	76	50	0.1457	24	14	22	5	10	7	4	8	3	8	17	11
Lamprolaima rhami	86	62	12	52	10	0.0717	7	6	8	9	16	18	5	4	0	1	0	0
Eugenes fulgens	10	8	0	2	6	0.0092	0	0	1	0	1	0	0	1	1	0	1	3
Doricha enicura	1	1	0	0	1	0.0012	0	0	0	0	0	0	0	0	0	1	0	0
Atthis ellioti	3	3	0	0	3	0.0035	0	0	0	0	0	0	0	0	0	0	3	0
Pharomachrus mocinno	1	1	0	1	0	0.0012	0	0	1	0	0	0	0	0	0	0	0	0
Asphata gularis	7	5	2	1	4	0.0058	1	0	0	0	0	0	2	4	0	0	0	0
Aulacorhynchus prasinus	1	1	0	0	1	0.0012	0	0	0	0	0	0	1	0	0	0	0	0
Picoides villosus	3	2	0	0	2	0.0023	0	0	0	0	0	0	0	2	0	0	0	0
Colaptes auratus	3	2	0	0	2	0.0023	0	0	0	0	0	0	0	1	0	1	0	0
Automolus rubiginosus	3	2	0	1	1	0.0023	0	0	0	1	0	0	1	0	0	0	0	0
Xiphorhynchus erythropygius	2	1	1	1	0	0.0012	0	0	2	0	0	0	0	0	0	0	0	0
Lepidocolaptes affinis	1	1	0	1	0	0.0012	0	0	1	0	0	0	0	0	0	0	0	0
Grallaria guatimalensis	1	1	0	1	0	0.0012	0	0	1	0	0	0	0	0	0	0	0	0
Camptostoma imberbe	1	1	0	0	1	0.0012	0	0	0	0	0	0	0	0	0	1	0	0
Zimmerius vilissimus	1	1	0	0	1	0.0012	0	0	0	0	0	0	1	0	0	0	0	0
Empidonax affinis	8	7	0	0	7	0.0081	0	0	0	0	0	0	3	0	0	1	3	0
Empidonax flavescens	22	18	2	10	8	0.0208	2	2	5	0	2	1	3	0	4	1	0	0
Vireo plumbeus	2	2	0	0	2	0.0023	0	0	0	0	0	0	0	0	1	1	0	0
Cyanocorax melanocyaneus	1	1	0	0	1	0.0012	0	0	0	0	0	0	0	0	0	1	0	0
Cyanolyca pumilo	3	3	0	3	0	0.0035	1	1	0	1	0	0	0	0	0	0	0	0
Thryothorus modestus	4	2	2	0	2	0.0023	0	0	0	0	0	0	0	0	1	1	2	0
Troglodytes musculus	9	6	1	0	6	0.0069	0	0	0	0	0	0	1	0	2	4	0	0
Troglodytes ruficiliatus	9	6	1	3	3	0.0069	0	1	0	0	1	1	0	0	0	3	1	0
Henicorhina leucophrys	47	28	12	19	9	0.0324	9	4	11	4	0	1	2	5	1	1	2	0
Myadestes occidentalis	31	22	4	1	21	0.0254	1	0	1	0	0	0	7	3	7	4	1	2
Myadestes unicolor	16	13	1	8	5	0.0150	3	0	3	2	0	1	0	3	2	0	0	0
Catharus aurantiirostris	8	2	1	2	0	0.0023	0	0	0	3	0	0	0	0	0	0	0	0
Catharus frantzii	114	63	35	41	22	0.0728	17	11	21	12	2	7	7	5	5	4	3	4
Turdus infuscatus	27	23	0	17	6	0.0266	2	4	4	5	0	2	0	3	0	1	1	1
Turdus plebejus	11	9	0	5	4	0.0104	1	0	1	0	1	2	1	0	1	1	1	0
Turdus grayi	4	3	0	3	0	0.0035	0	1	0	0	0	2	0	0	0	0	0	0
Melanotis hypoleucus	3	2	1	0	2	0.0023	0	0	0	0	0	0	1	0	1	1	0	0
Vermivora chrysoptera	1	1	0	0	1	0.0012	0	0	0	0	0	0	0	0	1	0	0	0
Parula superciliosa	2	1	0	1	0	0.0012	0	0	0	0	1	0	0	0	0	0	0	0
Dendroica fusca	1	1	0	0	1	0.0012	0	0	0	0	0	0	0	0	0	1	0	0
Oporornis tolmiei	4	3	1	0	3	0.0035	0	0	0	0	0	0	0	0	0	2	1	1
Geothlypis poliocephala	1	1	0	0	1	0.0012	0	0	0	0	0	0	0	0	0	0	1	0
Wilsonia pusilla	32	25	5	1	24	0.0289	1	0	0	0	0	0	0	3	7	3	13	3
Myioborus miniatus	4	2	2	0	2	0.0023	0	0	0	0	0	0	2	2	0	0	0	0
Basileuterus rufifrons	5	3	1	0	3	0.0035	0	0	0	0	0	0	0	0	1	0	3	0
Basileuterus belli	65	39	19	24	15	0.0451	6	5	10	8	5	1	4	16	1	1	1	0
Chlorospingus ophthalmicus	211	148	23	57	91	0.1711	16	14	14	8	9	5	30	9	46	6	4	10
Volatinia jacarina	2	2	0	0	2	0.0023	0	0	0	0	0	0	1	0	0	0	1	0
Sporophila torqueola	2	2	0	0	2	0.0023	0	0	0	0	0	0	0	0	1	0	1	0
Tiarias olivacea	6	6	0	0	6	0.0069	0	0	0	0	0	0	0	0	1	1	4	0
Diglossa baritula	74	45	21	8	37	0.0520	3	0	2	1	1	1	1	1	7	10	27	12
Atlapetes gutteralis	43	23	8	2	21	0.0266	0	0	2	0	0	0	8	1	7	8	2	3
Buarremon brunneinucha	50	31	7	6	25	0.0358	1	2	1	3	0	0	6	12	6	1	3	3
Melozone biarcuatum	2	1	0	0	1	0.0012	0	0	0	0	0	0	0	0	0	1	0	0
Zonotrichia capensis	2	2	0	0	2	0.0023	0	0	0	0	0	0	1	0	0	1	0	0
Aimophila rufescens	1	1	0	0	1	0.0012	0	0	0	0	0	0	1	0	0	0	0	0
Spizella passerina	2	2	0	0	2	0.0023	0	0	0	0	0	0	1	0	0	0	1	0
Ergaticus versicolor	1	1	0	1	0	0.0012	0	0	0	1	0	0	0	0	0	0	0	0
Carduelis notata	2	2	0	0	2	0.0023	0	0	0	0	0	0	0	0	0	1	1	0
Carduelis atriceps	2	2	0	0	2	0.0023	0	0	0	0	0	0	2	0	0	0	0	0

Appendix B

Figure 42: Typical image of the natural vegetation: (top left) canopy from below, (top middle) pine reforestation area of *Pinus maximinoii* (Pinaceae) with *Zea mays* in Chelemhá, (top right) Milpa (corn *Zea mays* Poaceae), (middle left) young secondary forest (middle right) natural forest gab, (bottom right) mist net at net line c, (bottom middle) natural vegetation, (bottom right) natural forest at forest edge.

Appendix C

Baseline data is available from the author.

Lebenslauf

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