

STRUCTURE OF A LOWLAND NEOTROPICAL GALLIFORM BIRD GUILD

By

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To my family, Michaelyn, Milano, and Chloe Lilyana

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Abstract of Thesis Presented to the Graduate School
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This study (1) examined guild structure, (2) compared guild characteristics to predictions from potentially relevant hypotheses of guild structure regulation, and (3) assessed the impacts of hunting on a guild comprised of the Great Curassow (*Crax rubra*), Crested Guan (*Penelope purpurascens*), Plain Chachalaca (*Ortalis vetula*), Ocellated Turkey (*Meleagris ocellata*), and the Great Tinamou (*Tinamus major*) in 2000-2002. The study area, located in the Maya Biosphere Reserve in northern Guatemala, included a national park unit with protected populations of the guild and an adjacent community concession unit subject to a range of subsistence hunting pressure. Diet niches and overlap were described from analyses of upper digestive tract contents from 267 *C. rubra*, 181 *M. ocellata*, 205 *O. vetula*, 142 *P. purpurascens*, and 55 *T. major* collected over a 24-month period. Descriptions of habitat niches and overlap, species abundance, and selected reproductive parameters were derived from line-transect sampling during a 30-month period in the park unit (1,770 km total) and over a 12-month period in the concession unit (995 km total). Descriptions of nest-sites, clutch-sizes, and other reproductive characteristics were based on observations made at 24 *C. rubra* nests, 39 *M. ocellata* nests, 77 *O. vetula* nests, 19 *P. purpurascens* nests, and 66 *T. major* nests.

Dry-mass proportions of grit were highest and similar in the diets of *M. ocellata* (22%) and *C. rubra* (20%), lowest and similar in *O. vetula* (2.7%) and *T. major* (2.2%), and intermediate in *P. purpurascens* (9%). Seeds and pulp represented the greatest and second-greatest proportions respectively, of the diet of all species when grit and snail shells were excluded from analyses. Overlap in the seed component of the diet ranged from 50-86% for eight of the ten species-pairs, and the average combined overlap exceeded 50% for all species except *O. vetula*. Habitat preferences were exhibited by *C. rubra* and *P. purpurascens* for tall-forest, and by *O. vetula* for low-forest. *T. major* occurred at a greater frequency in low-forest in the two areas with the least hunting pressure, and in high-forest in the two areas with the greatest hunting pressure. The frequency of occurrence of *M. ocellata* did not differ among habitat types. All species exhibited consistent vertical patterns of strata occupancy.

Guild characteristics were semi-consistent with structural regulation through competitive interactions with respect to habitat niches, body-size assortment, and evidence of competitive release, but were inconsistent with respect to diet niches and null-pool comparisons. The variability of habitat occupancy and abundance within the guild were consistent with expectations for non-equilibrium processes. Vertical stratification of nest-placement and other reproductive attributes of the guild were consistent with expectations for a guild subject to intense predation pressure. The guild appears to be a terrestrial vertebrate example of the non-equilibrium competition model of community structure proposed by Connell (1980). All species were most abundant in the fully-protected area; however, the abundance of *C. rubra*, *M. ocellata*, and *P. purpurascens* declined consistently along the increasing gradient of hunting pressure. Guild biomass in the most heavily hunted area represented 30% of the guild biomass in the protected area.

CHAPTER 1 INTRODUCTION

This study examines the structure of a lowland tropical bird guild composed of the Great Curassow (*Crax rubra*), Crested Guan (*Penelope purpurascens*), Plain Chachalaca (*Ortalis vetula*), Ocellated Turkey (*Meleagris ocellata*), and Great Tinamou (*Tinamus major*) in the El Petén department of Guatemala. These species share ecological and taxonomical or morphological similarities, and a limited size range that make them likely competitors (Root 1967; MacNally 1983). Three of the species, *C. rubra*, *P. purpurascens*, and *O. vetula*, are members of the family Cracidae, a Neotropical galliform family represented by 11 genera and 50 species that reaches maximum diversity in South America (Brooks & Strahl 2000). These three species are representative of the general size range of the family; *Ortalis* includes small cracid species, *Crax* large species, and *Penelope* intermediate-sized species. The largest species in the guild, *M. ocellata*, is also a galliform and the only tropical representative of the new world subfamily Meleagridinae. *T. major* belongs to the Neotropical family, Tinamidae which is most closely related to ratites. Tinamidae is represented by 9 genera and 47 species and also reaches greatest diversity in South America (Bertelli & Porzecanski 2004). Although not a galliform, *T. major* was included in this study because tinamids are ecologically similar to galliforms, and its size is consistent with the range of the guild (Thompson 2004; Brooks et al. 2004).

These species exist sympatrically in the forest-dominated landscape of the study area and share similar feeding habits. Although cracids have been described as frugivores (Karr 1971; Thiollay 1994) or granivores (Terborgh et al. 1990), diet studies have recognized the significance of seed, leaf, and animal materials (Santamaria & Franco 2000; Jimenez et al. 2001; Mamani-F 2001; Rivas & Morales 2003). Diet descriptions of *M. ocellata* indicate an omnivorous diet

dominated by seeds (Steadman et al. 1979). *T. major* diet has been described as granivorous (Thiollay 1994) or omnivorous (Howell & Webb 1995).

C. rubra is considered to function primarily as a seed predator on large-seeds and to a lesser degree as a disperser of small seeds (Santamaria & Franco 2000; Rivas & Morales 2003). Guans and chachalacas are considered to have lesser roles as seed predators and greater roles as dispersers than curassows (Brooks & Strahl 2000; Rivas & Morales 2003). *M. ocellata* has a muscular gizzard and consumes grit (Steadman et al. 1979) and likely functions more as a seed predator than a disperser. An assessment of the impacts of the diet of *T. major* was not available; however, due to its intermediate size relative to guans and chachalacas, the species is probably a lesser seed predator and greater disperser than the larger guild members.

Guilds of large galliform species are not well represented in literature regarding bird community structure and diversity. This under-representation may reflect less interest in generalist species, which may be less suitable for niche dimension research which has dominated community ecology, or may reflect vulnerability to hunting (Schoener 1983; Ricklefs 1990; Terborgh et al. 1990). Large galliform species are often reduced or extirpated where they are accessible, including sites where some of the most comprehensive field research of bird communities have been conducted (Karr 1971; Karr 1976b; Thiollay 1989; Terborgh et al. 1990). The Cracid Specialist Group of the International Union for the Conservation of Nature and Natural Resources (IUCN) describes Cracidae as the most threatened avian family in the Neotropics, ranking 24 of its 50 species in need of priority conservation efforts (Brooks & Strahl 2000). Although generally less abundant than smaller bird species, large galliforms may become common where protected (Thiollay 1989; Silva & Strahl 1991). Under natural conditions these species may represent significant proportions of the biomass of bird communities (Terborgh et

al. 1990; Redford 1992), and may qualify as “keystone trophic” components of tropical communities (Terborgh 1992). The combination of poor scientific representation, vulnerability, threatened status, and ecological significance of large galliform species emphasizes the need for research on such guilds where they persist under unexploited conditions (Terborgh et al. 1990; Thiollay 1994; Brooks & Strahl 2000).

Rahbeck and Graves (2001) cited 120 existing causal hypotheses of bird species-richness within the context of presenting yet a new model for predicting bird species-richness patterns. The tendency of tropical ecosystems to be more diverse than temperate systems, or “latitudinal diversity gradient”, may be the longest recognized pattern of species-richness (Hutchinson 1959; Pianka 1966; Gill 1990; Ricklefs 1990). Many hypotheses proposed to account for the structure of ecological communities, bird species-richness patterns, and the latitudinal diversity gradient are potentially relevant to the diversity and structure of this guild. Assessment of the relevance of any particular hypotheses is complicated by a variety of factors. Different hypotheses may predict similar local effects, may identify causal factors that are not mutually exclusive, or that may counteract one another. The interpretation of relationships among hypotheses varies among authors, and the same research findings are cited in support of distinct hypotheses among authors (Pianka 1966; Begon et al. 1990; Ricklefs 1990; Kricher 1997).

Regional-level hypotheses of tropical diversity generally emphasize the roles of abiotic or historical factors operating on temporal or spatial scales that are not amenable to testing based on the results of a single-site field study. Local-level tropical diversity hypotheses generally emphasize the causal roles of biotic factors or environmental variability. Biotic regulation of community structure may manifest as interspecific competition, external population controls, or resource heterogeneity (Begon et al. 1990; Ricklefs 1990). Local-level hypotheses generally

diverge with respect to variability, either regarding communities as equilibrium systems regulated by deterministic processes, or as non-equilibrium systems in which environmental factors counteract deterministic processes (Begon et al. 1990; Ricklefs 1990).

Regional-Level Diversity Hypotheses

The time hypothesis attributes greater tropical diversity to the historic stability of tropical biomes relative to temperate biomes subjected to glaciation during the Pleistocene (Begon et al. 1990; Ricklefs 1990). Evidence contrary to this hypothesis include: findings that tropical biomes were also subject to historic periods of expansion and contraction (Haffer 1969), that temperate biomes may be as old as tropical biomes (Ricklefs 1990) and that speciation can occur on temporal scales that are insignificant relative to biome age (Remsen 1990). Support for this hypothesis includes findings of comparisons of African and Neotropical bird communities in similar forest and savannah biomes in which bird community diversity was positively correlated to the relative age and historic extension of biomes (Karr 1976*b*).

The climatic stability and the productivity hypotheses attribute tropical diversity to reduced variability of abiotic factors such as temperature, precipitation, and solar radiation (Pianka 1966; Sanders 1968; Begon et al. 1990). Both hypotheses credit abiotic factors operating on regional levels with increased local diversity. Stable tropical climates are favorable to many plant and poikilothermic faunal taxa that in turn provide diverse and consistently available resources to consumers (Pianka 1966; Kricher 1997). The productivity hypothesis emphasizes the role of tropical stability in reducing physical stress on producers, permitting greater investment in non-maintenance activities such as reproduction, which results in greater abundance of producers and available resources to consumers (Connell & Orias 1964).

Local-Level Diversity Hypotheses

The regulation of community structure through competition has been a dominant paradigm in community ecology (Schoener 1974; Schoener 1983; Gill 1990; Ricklefs 1990). The competition hypothesis contends that when faunal communities are in a state of equilibrium, species will occupy distinct ecological niches (Hutchinson 1959). Greater local diversity in tropical systems increases interspecific competition, which becomes the most significant determinant of community structure. When community structure is regulated by competitive interactions, niche specialization is predicted to be prevalent among member species. Increased niche specialization permits ecological separation of competitors, which are expected to exhibit regular spacing along niche dimensions (Ricklefs 1990). According to this theory, modern tropical assemblages are diverse because increased niche specialization has resulted in “narrower” niches, thus accommodating greater numbers of species along resource gradients (Ricklefs 1990; Begon et al. 1990). Because modern assemblages represent species that have resolved historic competitive conflicts via co-adaptation, competition for resources may not occur except under conditions of extreme resource scarcity (Wiens 1977; Fleming 1979). The significance of competition may vary among trophic levels, with greater relevance to producers, decomposers, and predators than to herbivores, frugivores, and some omnivores (Hairston et al. 1960; Fleming 1979).

An alternative role of competition in the regulation of community structure predicts that competitive interactions in non-equilibrium systems will lead to greater niche generalization and overlap (Connell 1980). Competitive interactions are inconsistent when competitor abundance is highly variable or under conditions of diffuse-competition. Individuals of a given species may interact with distinct competitor species, or may not face consistent competition from any particular competitor species (Buckley 1983). This hypothesis contends that under such

conditions, species are more likely to develop evolutionary responses to food acquisition efficiency or mortality factors than to the niches of competing species.

Biotic environmental factors that maintain populations below carrying capacity create non-equilibrium conditions that prevent competitive interactions from reaching the point of competitive exclusion (Pianka 1966; Ricklefs 1990). The tropical diversity gradient applies to predators, parasites, and pathogens just as it does to other species. Predators often exhibit “*frequency-dependent selection*”, defined as the tendency to select the most abundant forms of prey. Parasites and pathogens are likely to increase in correlation to increased host populations. Because competitive exclusion does not occur under such conditions, communities may become more diverse (Ricklefs 1990; Kricher 1997). In assemblages of populations that are subject to external biotic controls it is predicted that species will exhibit lesser niche specialization and greater resource use overlap (Pianka 1966).

Abiotic environmental factors may create non-equilibrium conditions by reversing successional vegetation trends or by increasing resource variability. Forest-gap dynamics increase the heterogeneity of tropical forest diversity and structure (Connell 1978; Schemske & Brokaw 1981). Large rivers that flood seasonally maintain vegetation along the banks in early successional stages, increasing habitat heterogeneity and favoring greater bird diversity (Remsen & Parker 1983; Brooks et al. 2004). Highly variable precipitation patterns may reduce the availability or consistency of resources, limiting community diversity and precluding the development of niche specializations for particular resources (Karr 1976a).

Greater local diversity in the tropics may create resource gradients that are sufficiently heterogeneous to support a greater diversity of consumers (Hutchinson 1959; Kricher 1997). If resource heterogeneity is significant to community structure it is predicted that niches will

exhibit greater dimensionality (Ricklefs 1990). Habitat heterogeneity has been positively associated with bird species diversity in both tropical and temperate climates (MacArthur & MacArthur 1961; Karr & Roth 1971). The diversity of some tropical bird communities has been attributed to greater diversity of frugivorous, insectivorous, and nectivorous species, reflecting utilization of resources that are more diverse and abundant in the tropics (Pianka 1966; Karr 1971; Terborgh 1990).

Objectives

The primary objective of this study was to examine guild structure in a manner that would permit the assessment of relevant regulatory processes to the guild. Specific objectives were (1) to determine the degree of specialization of principal niche dimensions within the guild, (2) to determine the degree of ecological separation or overlap along corresponding resource gradients, and (3) to compare guild characteristics to predictions derived from potentially relevant hypotheses of structural regulation. The secondary objective of this study was to assess the impacts of hunting pressure on guild structure and composition.

Niches were described along certain dietary and habitat dimensions. Diet is considered the most essential niche dimension among terrestrial vertebrates (Schoener 1974; Schoener 1983) and dietary specialization has been documented in many tropical bird guilds (Ashmole 1968; Sherry 1984). Spatial separation along habitat resource gradients has been associated with the diversity of many bird communities (Cody 1968; Gill 1990). Habitat resources may be partitioned through preferential use, temporal variability of use, and vertical stratification (Gill 1990; Pearson 1971; Karr 1971).

Other guild characteristics that were compared to predictions based on potentially relevant hypotheses included size assortment, responsiveness of guild members to abundance variations of other guild species, guild membership, variability of species abundance and habitat

occupancy, and reproductive strategies. Size assortment is a mechanism of mitigating interspecific competition that occurs when combinations of similar species with distinct sizes persist better than similar-sized species (Case & Sidell 1983). Size assortment has been associated with the greater diversity of some tropical bird guilds (Ashmole 1968; Brooks 1998). If guild member populations are constrained by competitive interactions, then significant reductions of some species may offer an opportunity for competitive release to other guild members. The use of a greater range of habitat resources in the absence of competitors has been documented in some tropical bird communities (MacArthur et al. 1966). Bird populations are not static and significant temporal variations of abundance or habitat use may represent non-equilibrium factors that reduce the predictability of competitive interactions and counteract local processes of competitive exclusion (Karr & Freemark 1983; Gill 1990; Loiselle & Blake 1992). Vertical stratification of nest-placement is a mechanism of reducing nest-predation pressure through increased spatial distribution of nests (Martin 1988*a*; Martin 1993; Schmidt & Whelan 1998). Temporal separation of reproductive activities may mitigate interspecific competition for nesting or brooding resources in bird communities (Ricklefs 1966). Comparisons of guild composition to null pools of potential members that are regionally available have been used to assess the significance of competitive interactions to guild structure in tropical bird communities (Pearson 1977; Cornell & Lawton 1992).

It was predicted that if interspecific competition in the classic, equilibrium-system context is significant to the regulation of guild structure that: (1) species would have specialized niches, (2) species would exhibit regular spacing along niche dimensions, (3) species would be sufficiently different in size to mitigate competitive interactions, (4) species would exhibit some form of competitive release in response to significant variations in the abundance of other guild

members, (5) guild members might stagger reproductive activities to reduce competition for nesting and brooding resources, and (6) guild membership would include fewer similar species than are available from the regional null-pool of potential guild members.

Further it was predicted that if non-equilibrium processes were significant to guild structure, species would exhibit limited niche specialization and ecological separation, and populations would exhibit non-equilibrium properties such as significant temporal variations in abundance or habitat occupancy. Also it was predicted that if predation pressure was significant to guild structure then guild members would exhibit differential nesting strategies or reproductive traits that are adaptive to conditions of high mortality.

Conservation Threats

The “Maya Forest” refers to multinational complex of protected areas corresponding to the southern Yucatan peninsula regions of Mexico, Belize, and Guatemala. The Maya Forest is the largest Neotropical forest remnant in Mesoamerica encompassing approximately three-million hectares of contiguous forest cover (Radachowsky & Ramos 2004; CEMEC-CONAP 2006). The principal Guatemalan component of the forest is the Maya Biosphere Reserve (MBR) created in 1990 that includes over two-million hectares (CONAP 2001). Despite legal restrictions on the harvest of wildlife, law enforcement in Guatemala is minimal and hunting is largely uncontrolled. Throughout most of the MBR, these species are subject to persistent hunting pressure that is positively associated with permanent settlements and human access (Radachowsky & Ramos 2004). Some of the most isolated parts of the reserve continue to support unexploited populations of the guild species.

In 1960, the human population of the Petén was approximately 60,000, but has since doubled at approximately 8-year intervals (Meyerson 1997). A census of the Petén in 2001 recorded over 700,000 inhabitants, at which time there were approximately 90,000 residents

within the MBR (CONAP 2001). Since the declaration of its protected status, the MBR has lost over 2,000 km² of forest cover (Ramos et al. 2007) and been fragmented into distinct eastern and western forest blocks. Forest fires provoked by swidden (slash-and-burn) agricultural practices occur annually. The three worst fire seasons in the last 10 years were 1998, 2003, and 2005, during which 4,335 km², 3,985 km² and 3,752 km² respectively were affected by forest fires (Ramos et al. 2007).

The eastern forest block of the MBR retains approximately 8,000 km² of forest cover that links the Mexican and Belizean components of the Maya Forest. Current infrastructure proposals include three major road-building projects within this part of the reserve (Ramos et al. 2007). One proposed project is a highway that would connect Guatemala and Mexico through the best-conserved areas remaining in the eastern forest block. Environmental impact assessments of that project based on models from data on existing roads in the MBR (Ramos et al. 2007) predicted severe forest-cover loss, fragmentation into as many as three separate forests, and the loss of continuity between the Mexican and Belizean components of the Maya Forest by 2025 (Ramos et al. 2007).

Study Area

This study was conducted in two adjacent management units of the MBR; the community forestry concession of Uaxactún and the Mirador-Rio Azul National Park (Figure 1-1). The Uaxactún unit includes approximately 836 km² of the multiple-use zone and contains a single permanent settlement, the village of Uaxactún with approximately 700 residents (NPV-OMYC 1999). The Mirador-Rio Azul National Park encompasses approximately 1117 km² and is uninhabited (CONAP-ONCA-CECON 2002). The Mirador-Rio Azul National Park is divided into two sub-units, Mirador in the west and Rio Azul in the east. Data for this study were collected in the Rio Azul unit in the northeastern part of Guatemala bordering Mexico on the

northern perimeter, Belize on the eastern perimeter, and the Uaxactún unit on the southeastern perimeter.

Data from the nearest meteorological stations indicated mean monthly temperatures ranging from 23° C to 30° C (INSIVUMEH), being lowest November-February (mean median temperature = 26° C) and highest April-July (mean median temperature = 32° C). Local average annual precipitation is approximately 1250 mm. The annual precipitation pattern exhibits peaks in May or June and in September, and a four-month dry season from January-April.

The Uaxactún and Rio Azul units straddle the drainage basin of the Rio Tikal-Rio Hondo watershed. Elevation ranges from 100-400 m, the lowest areas corresponding to the drainage basin and the highest to a steep karst escarpment that borders the basin to the west and north. The eastern edge of the basin is characterized by isolated upland areas with gentle slopes. Seasonal flooding can be severe in low and poorly drained areas during the rainy season. Throughout the forest, small ponds that form in depressions during the rainy season often dry-up during the dry season, leading to seasonal scarcity of available surface water. The Rio Tikal River is an intermittent “*arroyo*” that only occasionally forms a current but retains small ponds year-round in depressions along the channel.

The landscape of the study area is dominated by a forest continuum that is classified as Subtropical Moist (Holdridge et al. 1971). A classification of the forest community in Tikal National Park, which is adjacent to the Uaxactún unit, found strong correlations of forest composition and structure to the edaphic conditions along the topographical gradient (Schulze & Whitacre 1999). Proceeding down the slope of this gradient, canopy height and basal area decrease and canopy opening size and stem-density increase (Schulze & Whitacre 1999).

Although 11 predictable forest-classes were identified along the topographical gradient, species richness and diversity were consistent among forest-classes (Schulze & Whitacre 1999).

The village of Uaxactún originated in the early 1900's as a collection center for “*chicle*”, the resin of the *Manilkara zapota* tree that was the original base ingredient of chewing-gum (NPV-OMYC 1999). Although the economic importance of gum-resin extraction has since diminished greatly, the local economy continues to be dominated by the extraction of forest resources including timber, palm fronds, allspice, construction materials, and wildlife. Although small-scale agriculture is locally important, deforested agricultural areas represent only 4% of the concession area (NPV-OMYC 1999). To accommodate extraction activities primitive camps interconnected by an extensive trail network are distributed throughout the concession.

Wildlife is harvested opportunistically during the course of other extractive and agricultural activities on a continuous basis. Community-based hunting pressure is inversely correlated to distance from the village (Polisar et al. 1998); however, camp-based extractive activities have temporary but intense impacts far from the village (McNab 1998; Morales & Morales 1998). Although subsistence hunting pressure is biased towards larger vertebrate species, individuals are generally harvested without regard to sex or age-class. Unpublished data provided by the Wildlife Conservation Society (WCS) in Guatemala indicated that the wildlife harvest in Uaxactún in 1997 produced approximately 10,400 kg of game meat, which would cost approximately \$30,000 US to replace with meat produced from domestic livestock. Given that the average annual household income is less than \$2,000 US (personal observation) among approximately 140 households in the village, the annual wildlife harvests represent a subsidy equivalent to more than 10% of the local economy.

CHAPTER 2 METHODS

Diet and Harvest Data

Data were collected from birds harvested for subsistence purposes by residents of the village of Uaxactún for the purpose of describing diet, body mass, and harvest pressure of guild species. The participating hunters provided upper-digestive tracts (gizzards and also crops when available) from harvested specimens along with relevant observations, for a reward equivalent to the value of a pound of game-meat (<1\$ US). Diet samples were separated from the tracts, dried in a solar dryer, and stored in paper envelopes in the community. Samples were dried again in electric dryers in the laboratory prior to processing. The contents of each sample were separated into distinct components for which dry mass values were recorded and identified on general and specific levels.

Diet compositions were based on the dry-mass proportions of general diet components including: animal, leaf, pulp, seed, flower/stem, and grit. For composition analyses unidentifiable pulverized material in each sample was assigned to the identifiable items according to their relative proportions. Alternative diet composition descriptions were determined without grit and snail shells, due to their bias relative to the dry mass of plant and animal tissues. Dietary-overlap indices were calculated for all species-pairs using the equation from Pianka (1973) shown below, based on the seed component of each species diets, where O_{jk} is the overlap between species j and species k , and P_{ij} and P_{ik} are the proportions of the i th resource used by the j th and k th species, respectively. Unidentifiable pulverized material was excluded from the overlap analyses.

$$O_{jk} = \frac{\sum_i^n P_{ij} P_{ik}}{\sqrt{\sum_i^n P_{ij}^2 P_{ik}^2}}$$

The harvest data reported by local hunters were used to describe local harvest pressure on guild member populations. Adult body-mass values from the data were applied to describe harvest biomass. Harvest pressure was described by distance per 4 km intervals from the village. Birds collected by local hunters are usually cleaned in the field to avoid spoilage and reduce the burden, so access to entire specimens was limited. Balance scales were provided to field personnel and certain local hunters in order to record body mass values from entire specimens opportunistically. Adult body-mass records were compared between species and sexes using an analysis of variance (ANOVA) and a Duncan's Multiple Range Test (alpha levels ≤ 0.05 were considered statistically significant). Size-ratios between closest-size species-pairs were compared to predictions from competition theory.

Line-Transect Data

A system of 12 line-transects (Buckland et al. 2001) provided data used to describe species abundance and certain niche parameters. Transects were organized into 4 groups of three, located along a hunting pressure gradient identified *a priori* (Polisar et al. 1998). The Ixcán transect group was located in the core of the Rio Azul unit where no hunting pressure was expected. The Cedro group was located on the park perimeter adjacent to the Uaxactún unit, approximately 25-37 km from the village where hunting pressure was expected to be light. The Uaxactún North group was located approximately 3-15 km north of the village where hunting pressure was expected to be heavy. The Uaxactún South group included the area surrounding the village where hunting pressure was expected to be heaviest.

Each transect within a group was located in a stratified-random manner in order to sample all forest-classes. In the Uaxactún unit, transects were oriented to avoid existing trails to reduce the probability of locals hunting on them. In the Rio Azul unit all but one of the transects were established on modified, existing trails. Eleven transects measured 2500 m, whereas one

transect measured 2750 m to improve representation of a forest-class in that group. Transects were flagged and labeled at 50 m intervals and mapped by forest-class.

Transects were sampled by trained observers between 0600 and 0930 hours at intervals of 5-10 days depending on personnel capacity, weather, and logistics. Observers recorded data from detections of guild members and other species of interest to associated researchers (Novack 2003; Garcia & Radachowsky 2003). The transects in the Rio Azul unit were established in February 2000 and sampled over a 30-month period. Each year data collection in Rio Azul was interrupted when seasonal flooding prevented access to the site. The transects in the Uaxactún unit were sampled from August 2000 through July 2001. The total sampling effort on all transects was approximately 2770 km.

Habitat Use

Habitat use was analyzed based on species-encounter rates by forest-class derived from the transect data. Two forest classifications based on alternative interpretations of the results of Schulze and Whitacre (1999) were evaluated. One classification consisted of three forest-classes: “Upland”, representing tall forest types on the upper slopes of the topographical gradient; “Scrub”, representing low forest types at the bottom of the gradient; and “Transitional”, representing intermediate forest types. The second classification consolidated the Upland and Transitional classes of the former classification into a single “Upland” forest-class, and used the same “Scrub” forest-class. Monthly species-encounter rates in the Upland and Transitional forest-classes of the three-class system were compared using a student t-test to determine if species responded to the increase resolution of that classification. To determine if species exhibited preferential habitat occupancy, species-encounter rates by forest-class were calculated for each transect group and annual period, converted into relative frequencies and compared using a student t-test. Alpha levels ≤ 0.05 were considered statistically significant for both t

tests. Habitat occupancy overlap was assessed using proportional similarity indices (Schoener 1970), calculated for each species-pair in each forest-class. For each species the combined average overlap with all other species was also described.

Coefficients of variation (CV) calculated from species-encounter rates were used to evaluate the temporal variability of habitat occupation. Monthly species-encounter rates by forest-class were plotted graphically and evaluated for temporal variations of habitat occupancy. Monthly species-encounter rates by forest-class were examined for correlation with precipitation, temperature, and encounter rates of other guild members using a Pearson correlation analysis.

Vertical Strata Occupancy

Vertical height records from the transect data were used to assess whether guild members exhibited consistent patterns of forest-strata occupancy. Height records were assigned to one of three categories, ground strata (0-1m), understory strata (1m to half of the mean canopy height), or canopy strata (half of the mean canopy height and above). The relative frequencies of occurrence in the three strata were compared between transect groups, forest-classes, and annual periods for each species using an analysis of variance (ANOVA) and a Duncan's Multiple Range Test (alpha levels ≤ 0.05 were considered statistically significant). Vertical overlap in strata occupancy was estimated for each species-pair using proportional similarity indices (Schoener 1970). For each species the combined average overlap with all other species was also described.

Species Abundance and Guild Composition

Variables derived from the transect data that were used to compare guild member abundance included individual-encounter rates, density estimates by forest-class, relative population size and relative population biomass. Monthly individual-encounter rates from the same annual period were compared among transect groups for each species using an analysis of variance (ANOVA) and a Duncan's Multiple Range Test (alpha levels ≤ 0.05 were considered

statistically significant). Density estimates were calculated from the transect data using the program DISTANCE version 5 (Thomas et al. 2005). Models used to estimate densities were selected by the program based on comparisons of all relevant combinations of detection functions. Data were adjusted (truncated or filtered) when necessary to control for data concentrations that were inconsistent with detection functions (“data heaping”).

Spatial forest-class descriptions derived from Landsat 7 (USGS/EROS 2000) satellite images from the study period were provided by CEMEC-CONAP (2006). Using the program ArcView 3.2 (ESRI 2000), 4 km-radius buffers representing 50 km² were applied to the approximate geographic center of each transect group and were used to determine habitat availability within the corresponding areas (Figure 1). Density estimates by forest-class were extrapolated by forest-class representations within each 50 km² area to estimate corresponding species population sizes. Guild composition descriptions for each transect group were determined based on relative population size and relative biomass representations at each site. Guild compositions were compared between transect groups and annual periods. Temporal variability of species abundance was assessed using coefficients of variation calculated from individual-encounter rates during annual and 30-month periods.

Nest Site Data

Data collected from nest-sites of guild members were used to determine reproductive characteristics of each species. Local participants were compensated a day’s wage (approximately \$7 US) to accompany data collectors to nests encountered during the course of other activities and to assist with data collection at the nest site. Clutch sizes were included in analyses if they met the minimum clutch size reported from a literature source, and did not appear abandoned. Search effort was not systematic with respect to habitat so forest-class percentages are not representative of habitat distributions for the species. Nest sites could only

be visited once and some visits were made after nesting activities had concluded so nest depredation and clutch-size records are conservative. Vertical nest placement, tree diameter, and clutch-size were compared between species using an analysis of variance (ANOVA) and a Duncan's Multiple Range Test (alpha levels ≤ 0.05 were considered statistically significant). Nest placement patterns within the guild were evaluated for spatial separation. Temporal patterns of reproductive activities were described from field observations, the line-transect and the nesting data and subsequently evaluated for temporal separation.

CHAPTER 3 RESULTS

Diet Composition and Overlap

Diet content samples were derived from 267 *C. rubra*, 181 *M. ocellata*, 205 *O. vetula*, 142 *P. purpurascens*, and 55 *T. major* (Table 3-1). Grit represented 20% of the diet in *C. rubra*, 22% in *M. ocellata*, 3% in *O. vetula*, 9% in *P. purpurascens*, and 2% in *T. major*. Diet compositions without grit and snails indicated seed proportions of 88% of the diet in *C. rubra*, 77% in *M. ocellata*, 85% in *O. vetula*, 88% in *P. purpurascens*, and 90% in *T. major*. Excluding grit and snails, fruit pulp comprised 8% of the diet in *C. rubra*, 11% in *M. ocellata*, 7% in *O. vetula*, 10% in *P. purpurascens*, and 7% in *T. major*. Leaf proportions without grit and snails contributed 10% of the diet in *M. ocellata*, 7% in *O. vetula*, and less than 2% of the diets of the remaining species. Proportions of flower/stem and animal materials varied among species, but were less than 3% of the diet of any guild member.

Guild diet included 143 seed species, with similar quantities among guild members despite sample size differences: *C. rubra* (74 spp.), *M. ocellata* (92 spp.), *O. vetula* (86 spp.), *P. purpurascens* (72 spp.), *T. major* (67 spp.). Seed-species overlap values between species-pairs ranged from 33% for *M. ocellata*-*O. vetula* to 86% for *C. rubra*-*T. major* (Table 3-2). Average seed overlap with all other species ranged from 47-68%, with *T. major* ranking highest, followed in sequential order by *P. purpurascens*, *C. rubra*, *M. ocellata*, and *O. vetula*.

Harvest Description

The recorded harvest of guild members averaged 591 individuals representing 1625 kg of biomass annually based on average adult, body-mass of guild members. *C. rubra* represented an average of 47% of the total harvest and 58% of the harvest biomass annually. *M. ocellata* represented 19% of the total harvest and 28% of the biomass the first year, and declined to 13%

and 22% respectively, the second year. *O. vetula* represented 16% of the harvest and 3% of the biomass the first year, and increased to 25% and 6%, respectively, the second year. *P. purpurascens* represented 7% of the harvest and 6% of the biomass the first year, and increased to 17% and 16%, respectively, the second year. *T. major* represented an average of 5% of the annual harvest and 2% of the biomass. Harvest pressure on *C. rubra*, *M. ocellata*, and *P. purpurascens* was greatest in the second distance-interval (4-8 km) from the village and declined steadily in subsequent intervals. Harvest pressure on *O. vetula* and *T. major* was greatest in the first distance interval (0-4 km) and declined steadily in subsequent intervals.

Size Assortment

Adult body-mass records were collected from 67 *C. rubra*, 29 *M. ocellata*, 17 *O. vetula*, 26 *P. purpurascens*, and 12 *T. major*. Average adult body-mass was 3.4 kg for *C. rubra*, 4.16 kg for *M. ocellata*, 0.64 kg for *O. vetula*, 2.31 kg for *P. purpurascens*, and 1.17 kg for *T. major*. Adult body-mass differed between guild members based on the results of both analyses (ANOVA, $\alpha = 0.0001$, $F = 336.91$, $df = 150$; Duncan's, $\alpha = 0.05$, $df = 146$). Adult body-mass of sexes differed in *M. ocellata* (male = 4.81 kg; female = 3.51 kg) (ANOVA, $\alpha = 0.0001$, $F = 26.79$, $df = 28$; Duncan's, $\alpha = 0.05$, $df = 27$) and *P. purpurascens* (male = 2.16 kg; female = 2.44 kg) (ANOVA, $\alpha = 0.0269$, $F = 5.56$, $df = 25$; Duncan's, $\alpha = 0.05$, $df = 24$). Size ratios (and natural logarithm equivalents) between species-pairs were 1.23:1 (0.209) for *C. rubra*-*M. ocellata*, 1.47:1 (0.384) for *C. rubra*-*P. purpurascens*, 1.98:1 (0.681) for *P. purpurascens*-*T. major*, and 1.83:1 (0.609) for *O. vetula*-*T. major*. Size ratios between *M. ocellata* sexes and *C. rubra* were 1.42:1 (0.348) for males and 1.03:1 (0.032) for females.

Habitat Use

Monthly species-encounter rates between Upland and Transitional forest-classes did not differ for any guild member. All subsequent habitat comparisons were made using the two

forest-class system. Frequencies of occurrence between forest-classes were unequal ($\alpha = 0.0001$) for *O. vetula* ($t = -7.9141$, $df = 10$), *C. rubra* ($t = 11.681$, $df = 10$), and *P. purpurascens* ($t = 6.1134$, $df = 10$) and nearly unequal ($\alpha = 0.0601$) for *T. major* ($t = 2.1193$, $df = 10$). *M. ocellata* did not differ in forest-class occupancy. *O. vetula* occurred in Scrub forest with an average frequency of 0.77. *C. rubra* and *P. purpurascens* and *T. major* occurred in Upland forest with average frequencies of 0.73, 0.66, and 0.58, respectively. Habitat overlap among species-pairs ranged from 27-48% in Scrub forest and from 23-67% in Upland forest (Table 3-3). Combined habitat overlap among species-pairs ranged from 50-94%. Average combined habitat overlap with all other species ranged from 61-84%, with *T. major* ranking highest, followed in sequential order by *M. ocellata*, *P. purpurascens*, *C. rubra*, and *O. vetula*.

Ratios of CV values between Scrub forest and Upland forest were 1.82:1 for *C. rubra*, 1.35:1 for *M. ocellata*, 2.35:1 for *P. purpurascens*, and 1.94:1 for *T. major*, indicating greater variability in the occupancy of Scrub forest. The CV ratio between Upland forest and Scrub forest was 1.43:1 for *O. vetula* indicating greater variability in the occupancy of Upland forest. Graphical analyses of monthly species-encounter rates by forest-class did not reveal any consistent temporal trends or shifts in forest-class occupancy by guild members. The Pearson correlation analyses did not identify any ($\alpha = 0.05$) correlations of monthly species-encounter rates with respect to temperature, precipitation, or encounter rates of other species.

Vertical Strata Occupancy

All species exhibited differential use of forest strata (ANOVA $df = 35$): *Crax rubra* ($\alpha = 0.0011$, $F = 4.68$), *M. ocellata* ($\alpha = 0.0001$, $F = 43.07$), *O. vetula* ($\alpha = 0.0018$, $F = 4.36$), *P. purpurascens* ($\alpha = 0.0001$, $F = 43.41$), *T. major* ($\alpha = 0.0001$, $F = 57$).

Vertical patterns of forest-strata occupancy did not differ between transect groups, forest-classes, or annual periods for any species (Duncan's $\alpha = 0.05$, $df = 27$) *M. ocellata* and *T. major* had

average frequencies of 89% and 92%, respectively, in the ground stratum. *C. rubra* had an average frequency of 59% in the canopy stratum and an average of 32% in the ground stratum. *P. purpurascens* had an average frequency of 84% in the canopy stratum. *O. vetula* had average frequencies of 53% and 41%, respectively, in the canopy and understory strata. Vertical strata overlap ranged from 14% between *O. vetula*-*T. major* to 93% between *M. ocellata*-*T. major* (Table 3-4). Four species-pairs exhibited vertical overlap greater than 50%. Average combined overlap with all other species ranged from 40-56%, with *C. rubra* ranking highest, followed in sequential order by *M. ocellata*, *P. purpurascens*, *O. vetula*, and *T. major*.

Species Abundance and Guild Composition

Monthly individual-encounter rates differed (Duncan's, $\alpha = 0.05$, $df = 42$) among transect groups for *C. rubra* (ANOVA, $\alpha = 0.0001$, $F = 9.13$, $df = 45$), *O. vetula* (ANOVA, $\alpha = 0.0012$, $F = 6.36$, $df = 45$), and *P. purpurascens* (ANOVA, $\alpha = 0.0001$, $F = 31.49$, $df = 45$). Encounter rates decreased along the increasing hunting gradient for *C. rubra*, *M. ocellata*, and *P. purpurascens*. Encounter rates were highest in the Ixcan and Uaxactún South groups for *O. vetula*. Encounter rates were highest in the Ixcan group and stable among the remaining transect groups for *T. major*.

Density estimates for all species were highest in the protected Ixcan group (Table 3-5). Density estimates generated by DISTANCE for some species in the less hunted areas seemed intuitively robust, however the results of analyses were ultimately accepted if they met the model selection criteria of the program, were consistent with the data and derived encounter-rates, and were comparable published density estimates for these or congeneric species.

C. rubra exhibited overall density declines along the increasing hunting gradient by 83% in both Upland and Scrub forest. *M. ocellata* exhibited overall declines along the increasing gradient of approximately 66% both forest-classes, with highest density estimates in the Ixcan

and Uaxactún North groups. *O. vetula* densities were similar and highest in the Ixcan and Uaxactún South groups. *P. purpurascens* exhibited an overall decline along the gradient of 72% in Upland forest and 43% in Scrub forest. *T. major* exhibited little density variation among the Cedro, Uaxactún North and Uaxactún South transect groups. *T. major* exhibited higher densities in Scrub forest relative to Upland forest in the Ixcan and Cedro groups, and higher densities in Upland forest relative to Scrub forest in the two Uaxactún groups. Comparison of densities between years in the Ixcan and Cedro groups indicated increased or stable densities among all species, except for slight decreases for *T. major* in the Cedro group. Between years the estimated density of *M. ocellata* increased by 59% in Upland forest and 14% in Scrub forest in the Ixcan group, and by 159% in Upland forest and 569% in Scrub forest in the Cedro group.

C. rubra represented proportions of the guild ranging from 24-32% in the Ixcan, Cedro, and Uaxactún North groups, but only 11% in the Uaxactún South group (Table 3-6). *M. ocellata* averaged 18% of the guild in the Ixcan and Uaxactún North groups, and 10% and in the Cedro and Uaxactún South. *O. vetula* averaged 24% of the guild in the Ixcan, Cedro, and Uaxactún North groups and represented 46% of the guild in the Uaxactún South group. *P. purpurascens* averaged 23% of the guild in the Ixcan and Cedro groups, and 14% in the two Uaxactún groups. *T. major* averaged 10% of the guild in the Ixcan and Cedro groups and 19% in both Uaxactún groups.

C. rubra accounted for the highest biomass proportion of the guild in all groups (average 40%) except Uaxactún South where it represented only 22%. *M. ocellata* averaged 31% of the guild biomass in all transect groups except the Cedro group where it accounted for only 18%. The proportions of guild biomass represented by *O. vetula* increased steadily along the increasing hunting gradient from 6% in the Ixcan group to 18% in the Uaxactún South group. *P.*

purpurascens accounted for 25% of guild biomass in the Cedro group, 21% in the Ixcan and Uaxactún South groups, and 14% in the Uaxactún North group. *T. major* accounted for 5% of guild biomass in the Ixcan and Cedro groups and an average of 12% in the two Uaxactún groups.

Coefficients of variation calculated from individual-encounter rates during both annual and 30-month periods indicated double-digit percentage changes for all species. Average CVs for annual periods were 34% for *C. rubra*, 35% for *M. ocellata*, 26% for *O. vetula*, 18% for *P. purpurascens*, and 21% for *T. major*. CVs of variation for the 30-month period were 38% for *C. rubra*, 62% for *M. ocellata*, 32% for *O. vetula*, 22% for *P. purpurascens*, and 22% for *T. major*.

Nest Site and Clutch Characteristics

A total of 225 were observed: *C. rubra* nests ($n = 24$), *M. ocellata* nests ($n = 39$), *O. vetula* nests ($n = 77$), *P. purpurascens* nests ($n = 19$), *T. major* nests ($n = 66$). Mean nest height differed for *O. vetula* (5.7 m, range 1-18 m), and species pairs *C. rubra* (10 m, range 5-25 m) -*P. purpurascens* (9.75 m, range 4-15 m), and *T. major* (0 m) -*M. ocellata* (0 m) ($\alpha = 0.05$, $df = 206$). Mean DBH of trees associated with nest sites differed between the species group *T. major* (35.4 cm) -*M. ocellata* (32.3 cm) -*P. purpurascens* (26.3 cm) and the individual species *C. rubra* (20 cm) and *O. vetula* (16.9 cm) ($\alpha = 0.05$, $df = 151$).

Mean clutch sizes for *M. ocellata* (8.73, mode = 9) and *T. major* (4.49, mode = 4) differed from each other and the other guild members ($\alpha = 0.05$, $df = 203$). Mean clutch sizes for *P. purpurascens* (2.16, mode = 2) -*O. vetula* (2.12, mode = 2) -*C. rubra* (2.00, mode = 2). Depredation of nests, based on a single visit, were 20% ($n = 13$) for *T. major*, 15% ($n = 6$) for *M. ocellata*, 4% ($n = 3$) for *O. vetula* nests, 4% ($n = 1$) for *C. rubra*, and 0% for *P. purpurascens*. With respect to habitat, 96% ($n = 23$) of *C. rubra* nests, 95% ($n = 19$) of *P. purpurascens* nests, 95% ($n = 23$) of *T. major* nests, 36% ($n = 14$) of *M. ocellata* nests, and 16% ($n = 12$) of *O. vetula* nests were located in Upland forest. Nesting in Scrub forest was only

observed for *O. vetula* (7%), *T. major* (5%), and *M. ocellata* (3%). Only *O. vetula* (78%) and *M. ocellata* (62%) nests were observed in agricultural habitat.

Specifically, all *C. rubra* and *P. purpurascens* nests were placed in trees, and all *T. major* nests in the roots of trees. Seventy-three percent ($n = 52$) of *O. vetula* nests were placed in trees, 20% ($n = 14$) were in vines. *M. ocellata* placed 49% ($n = 19$) and 36% ($n = 14$) of their ground nests in bracken fern (*Pteridium* spp.) and the roots of trees, respectively.

All guild members commenced nesting near the end of the dry season (March-April) and continued into the wet season; however, the length of the nesting period varied among guild members (Table 3-7). Active nests of *C. rubra* and *M. ocellata* were only observed April-June, whereas nests of *P. purpurascens* were observed from April-July. Nesting by *T. major* and *O. vetula* occurred during March-September and March-October, respectively.

CHAPTER 4 DISCUSSION

Guild Diet Characteristics

Relatively high proportions of grit in the diets of *C. rubra* and *M. ocellata* suggest that they function as seed predators. Relatively low proportions of grit in the diets of *O. vetula* and *T. major* suggest that they function less as seed predators than the rest of the guild. Diet compositions of *C. rubra*, *O. vetula*, and *P. purpurascens* were similar to previous findings (Rivas & Morales 2003). Flower and stem materials combined did not represent a significant proportion of the diet of any guild member. Flowers have been reported in higher proportions in the diets of *P. purpurascens* (Rivas & Morales 2003), and *M. ocellata* (Steadman et al. 1979), and may be seasonally important to curassows (Santamaria & Franco 2000). Animal matter was proportionately higher in *M. ocellata* with snail shells included, but similar to other species when they were excluded. Diet studies based on direct observations indicate frequent consumption of a variety of small vertebrates by curassows (Santamaria & Franco 2000, Jimenez et al. 2001). The relatively higher proportions of leaf material in the diets of *M. ocellata* and *O. vetula*, in contrast to the other guild members, are consistent with findings from other studies (Rivas & Morales 2003; Steadman et al. 1979). Excluding grit and snails, the diet of individual guild members had similar proportions of pulp (7-11%) and of seeds (77-90%), thus the diet of this guild is dominated by seeds, many of which are consumed as whole fruit.

Species-pairs *O. vetula*-*M. ocellata* and *C. rubra*-*O. vetula* displayed relatively low dietary overlap (33% and 39% respectively), two species-pairs, *P. purpurascens*-*T. major* and *C. rubra*-*T. major* displayed relatively high overlap (73% and 86% respectively), and the remaining six species-pairs had intermediate values (50-68%). Of the 143 seed species consumed by guild members; 19% (27 seed species) were shared by all five guild members, 13% (19) by four

members, 18% (26) by three members, and 21% (30) were shared by two guild members. Seed species shared by the entire guild represented significant proportions of the diets of individual species: 82% of the seed dry mass in *C. rubra*, 76% in *M. ocellata*, 57% in *O. vetula*, 79% in *P. purpurascens*, and 83% in *T. major*. The fruits *Brosimum alicastrum* and *Psuedolmedia* spp. were among the top-five ranking seeds in the diets of four of the guild members and ranked 15th and 8th, respectively, in *O. vetula*.

Rivas & Morales (2003) analyzed diets of *C. rubra*, *O. vetula*, and *P. purpurascens* collected from the study area between January 2002 and July 2003. In that study the two most significant seed species in the diet of *C. rubra* were from the fruits *Pouteria amygdalina* (47%) and *Protium copal* (8%); the two most significant seeds in the diet of *P. purpurascens* were *P. amygdalina* (17%) and *Vitex gaumeri* (12%); and the most significant seed in the diet of *O. vetula* was *Psuedolmedia* spp. (19%). In the current study *P. amygdalina* represented 9% and *P. copal* 1% in *C. rubra*; *P. amygdalina* represented 1% and *V. gaumeri* 5% in *P. purpurascens*; and *Psuedolmedia* spp. represented 3% in *O. vetula*.

In the current study, the most significant seed species in the diet of *C. rubra* were *B. alicastrum* (20%) and *Calophyllum brasiliensis* (19%), and the most significant seed species in the diet of *P. purpurascens* was *Chrysophylla argentea* (14%). Rivas and Morales (2003) did not detect *B. alicastrum* in the diet of *C. rubra* and *C. brasiliensis* represented 6% of the diet furthermore they found that *C. argentea* represented 5% of the diet in *P. purpurascens*. Those authors noted only minor representation of *B. alicastrum* which represented (3%) in *O. vetula* and (0.05%) in *P. purpurascens*. Rivas (1995) analyzed diet contents of *C. rubra* from the same area in 1995 and identified *B. alicastrum* as the most important diet species.

In summary members of this guild members consume many of the same seed species, some of which are important to the diet of most members of the guild. Common usage of important seed species by guild members suggests that food resources were not limited. The contrasting results of these two studies indicate that the importance of seed species varies with time. Temporal variability in the importance of some seeds may reflect variability in production due to fluctuations in annual precipitation. To illustrate, Peters (1989) found that fruit production of *B. alicastrum* is strongly correlated with precipitation. Local meteorological data indicated mean annual variations in precipitation of 200mm (16% of annual mean) with extremes of as much as 800mm (64% of annual mean).

Guild Habitat Characteristics

Overall guild occupancy was greatest in Upland forest, which may reflect a greater volume of habitat space relative low-canopy Scrub forest. Habitat occupancy patterns of *O. vetula*, *C. rubra*, and *P. purpurascens* were consistent between transect groups and annual periods, and highly skewed towards a particular forest-class, indicating habitat selection by these species. Preferential habitat use was exhibited by all six cracid species in a similar guild in Bolivia (Wallace et al. 2001). Preferential occupancy of Scrub forest by *O. vetula*, and of Upland forest by *C. rubra* and *P. purpurascens* were consistent with habitat-use descriptions for the species (Gonzalez et al. 1998; Howell & Webb 1995; Brooks et al. 2004). Open, grassy clearings have been identified as important habitat for reproductive activities and feeding for *M. ocellata*, and are known to be important brooding habitat for *M. gallopavo* in North America (Steadman et al. 1977; Gonzalez et al. 1998; Williams & Austin 1988). Open, grassy clearings are almost nonexistent in the study area therefore local habitat may not be optimal for *M. ocellata*.

Overlap values calculated using the proportional similarity index are expected to be conservative (Krebs 1989). The two species that exhibited the strongest and most divergent habitat preferences were *O. vetula* and *C. rubra*, which subsequently had the lowest combined habitat overlap among species-pair with 50%. The species-pairs with the most similar patterns of habitat use, *M. ocellata*-*T. major* and *C. rubra*-*P. purpurascens*, shared the highest overlap values in the guild at 94%. Based on that range, three other species-pairs (*P. purpurascens*-*T. major*, *M. ocellata*-*P. purpurascens*, and *C. rubra*-*T. major*) had high combined habitat overlap (85-91%), two species-pairs (*M. ocellata*-*O. vetula*, *C. rubra*-*M. ocellata*) had intermediate overlap (71-79%), and two species-pairs (*O. vetula*-*P. purpurascens*, *O. vetula*-*T. major*) had low overlap (56-65%).

All species that exhibited habitat preferences also exhibited greater variability of occurrence in the alternative forest-class. *M. ocellata* exhibited the most variability in habitat occupancy and the least. *C. rubra*, *O. vetula*, and *P. purpurascens* exhibited similar variability of habitat occupancy. Despite variability of habitat occupancy among all species, consistent temporal patterns of differential habitat occupancy were not exhibited by any guild member. The latter finding is in contrast with seasonal habitat shifts reported for *M. ocellata* by Gonzalez et al. (1998).

Consistent and distinct patterns of vertical strata occupation indicate vertical stratification within the guild, which is considered to be important in tropical bird communities (Karr & Roth 1971; Pearson 1971). The vertical patterns of strata occupation exhibited by guild members were consistent with descriptions for these species (Howell & Webb 1995; Brooks et al. 2004).

Relevance of Competition to Guild Structure

Diet compositions, high diversity of dietary resources, and significant dietary overlap among most species-pairs indicate generalist diet niches for all guild members. The hypothesis

that guild members have specialized dietary niches is not supported by the data. The only evidence of differential dietary resource use in the guild were the proportionally greater leaf material in the diets of *M. ocellata* and *O. vetula*, and the low overlap values between species-pairs *O. vetula-M. ocellata* and *C. rubra-O. vetula*. The hypothesis that the guild members exhibit regular spacing along a gradient of dietary resources is not supported by the comparisons of guild member diets.

Differential habitat preferences between *O. vetula* and the two larger cracids indicate specialized use of habitat by these three species. The limited habitat preference exhibited by *T. major* and the lack of preference exhibited by *M. ocellata* suggest generalist habitat resource use by these species. The hypothesis that the guild members have specialized habitat niches is only partially supported by the data. Less selective use of habitat by *M. ocellata* and *T. major* increased the representation of the guild in Scrub forest, and may represent deliberate spatial separation from *C. rubra* and *P. purpurascens* populations in Upland forest. Overall habitat occupancy patterns among all species indicate spatial separation along a gradient of habitat resources. The hypothesis that the guild exhibits regular spacing along the gradient of habitat resources is supported by comparisons of habitat occupancy patterns.

The hypothesis that guild members would have specialized niches with respect to the vertical occupation of forest strata is supported by the consistent patterns exhibited by all species. The hypothesis that the guild exhibits regular spacing along a vertical gradient of forest strata is supported by the vertical stratification observed within the guild.

Size ratios in a community structured by competitive interactions are predicted to be either constant, have minimum values from 1.6-2.0:1 (natural logarithm values between 0.405 and 0.683), or else to increase with species size (Hutchinson 1959; Diamond 1962; Oskanen et

al. 1979). Ratios of size differences between guild members are not constant and decrease among the largest three species. The size differences between species-pairs *P. purpurascens*-*T. major* (0.681) and *T. major*-*O. vetula* (0.609), were similar and also consistent with predicted minimum differences. The size differences between species-pairs *M. ocellata*-*C. rubra* (0.209) and *C. rubra*-*P. purpurascens* (0.384), are not similar to one another or to the size differences between other species-pairs, and are less than predicted minimums in assemblages structured by competitive interactions. The hypothesis that size assortment of the guild is sufficient to mitigate competitive interactions is supported by size differences among half of the guild species.

C. rubra, *M. ocellata*, and *P. purpurascens* populations exhibited significant reductions along the increasing hunting pressure gradient. *O. vetula* and *T. major* abundance did not increase significantly nor did they exhibit changes in vertical strata occupancy in the transect group where *C. rubra*, *M. ocellata*, and *P. purpurascens* populations were most reduced. *T. major* exhibited a relative shift in habitat occupancy from Scrub forest in the two groups where hunting pressure was light, to Upland forest in the two groups where hunting pressure heavy. Considering that *T. major* had the lowest relative abundance in the transect groups where hunting pressure was light and exhibited the highest overlap with all other species in dietary and habitat resources, it may experience the greatest competitive pressure from the other species. *T. major* was the only species that exhibited an inter-annual density decrease in the Cedro group, where *M. ocellata* concurrently exhibited extraordinary density increases, which may indicate competitive inhibition of *T. major* by *M. ocellata*. These two species had the highest overlap in the guild along diet and vertical niche dimensions as well as relatively high dietary overlap. The hypothesis that guild members would exhibit competitive release in response to the decreased abundance of other species is partially supported by the data.

Although guild members exhibited variable nesting period lengths, reproductive activities peaked during the same time of year for all guild members. The hypothesis that guild members may stagger reproductive activities to avoid competition was not supported from the temporal nesting patterns exhibited by the guild.

Aside from the five existing guild members, the only potential guild members available within a 200 km radius are the Horned Guan (*Oreophasis derbianus*), the Highland Guan (*Penelopina nigra*), and the White-bellied Chachalaca (*Ortalis luecogastra*). The two guans are not legitimate null pool species because they are highland species with lower distribution limits at elevations of 1000 m for *Penelopina* and 2000 m for *Oreophasis*. Although *O. luecogastra* exists at low elevations, regional *Ortalis* species were previously considered con-specific, and current taxonomic descriptions reflect distinct geographic distributions (Howell & Webb). Because regional *Ortalis* species are geographically separate, they may not qualify as legitimate null pool species capable of colonizing a distinct geographic area. *O. luecogastra* is confined to the Pacific slope of the isthmus, which is separated from the study area by mountain ranges along the entire length of the species distribution, so the absence of the species in the study area is not likely to be the result of competitive exclusion. A regional null pool including *O. luecogastra* would consist of only six species, in which case the local absence of *O. luecogastra* could be attributable to competitive exclusion by *O. vetula*. If *O. luecogastra* is excluded from the regional null pool, then all available potential guild members are represented locally. Competitive interactions within the guild do not appear sufficient to exclude regionally available guild members except possibly in the case of *O. luecogastra*. The hypothesis that the guild would include fewer similar species than are regionally available is not supported based on null pool comparisons.

Guild characteristics are partially consistent with predictions based on competition theory in an equilibrium system. Guild members exhibited niche specialization with respect to vertical occupancy of forest strata, and to some degree with respect to habitat use, but did not exhibit niche specialization with respect to the use of dietary resources. Guild members appeared to be ecologically separated along habitat resource and vertical forest strata gradients, but not along the gradient of dietary resources. Size differences appeared to be sufficient to mitigate competitive interactions for *O. vetula*, *T. major*, and *P. purpurascens*, but not for *C. rubra*, *M. ocellata*, and *P. purpurascens*. Overlap between *C. rubra*, and *P. purpurascens* was relatively high along all niche dimensions. Overlap between *M. ocellata* with both *C. rubra* and *P. purpurascens* was relatively high with respect to habitat and dietary resources and low with respect to vertical strata use. If competitive interactions were significant within the guild, *C. rubra*, *M. ocellata* and *P. purpurascens* would be expected to exhibit greater specialization and separation along the other niche dimensions. *T. major* exhibited inverse responses to variations of the abundance of other guild members. Guild membership was not notably different from the regional null pool. Although some guild characteristics are consistent with an assemblage structured by competitive interactions, the degree is less than would be expected based on predictions from competition theory in an equilibrium system. The limited evidence of competitive interactions displayed by the guild may be consistent with the non-equilibrium competition model proposed by Connell (1980).

Relevance of Non-Equilibrium Factors to Guild Structure

Niches should evolve in response to mortality factors and dietary resources as well as competition, therefore some niche specialization and ecological separation would be expected whether or not competitive interactions are important to the guild. Guild member niches were generalist with respect to diet, semi-specialized with respect to habitat, and specialized with

respect to vertical occupation of forest strata. The guild did not exhibit ecological separation with respect to dietary resources, but did appear to be distributed along habitat and vertical strata dimensions. The hypothesis that guild species would exhibit limited niche specialization and separation along niche dimensions is supported by the niche characteristics of the guild.

Significant temporal variability of guild member abundance would constitute environmental non-equilibrium. CVs of individual-encounter rates during annual and 30-month periods represented double-digit percentages for all species. Although an objective basis of comparison of the coefficient values is not available, these percentages appear to represent significant variation in guild member abundance. CVs were consistently highest for *C. rubra* and *M. ocellata*, which may reflect greater movement in foraging strategies. Significant local temporal variation of curassow abundance has been attributed to movement between patchy fruit resources (Thiollay 1989). CVs were relatively consistent between inter-annual and the 30-month periods for all species except *M. ocellata*, which had a much higher coefficient for the 30-month period. This observation suggests that inter-annual variation may be greater than intra-annual variation in this species. Inter-annual changes of guild member densities in the two, Rio Azul transect groups also indicated significant variation of abundance for all species. The hypothesis that guild members may exhibit significant variation in abundance is supported by the variability exhibited by individual-encounter rates and density estimates.

Temporal shifts in habitat use by bird species in response to microhabitat variability may result in dynamic assemblages representing non-equilibrium environmental factors (Karr & Freemark 1983). The CVs of species-encounter rates in Upland and Scrub forests indicated considerable variation of habitat occupancy. The hypothesis that guild members may exhibit significant variation in habitat occupancy is supported by the variation observed from species-

encounter rates in each forest-class. In summary the combination of limited niche specialization and ecological separation and the high variation of species abundance and habitat occupancy, are consistent with predictions of non-equilibrium systems.

Relevance of Predation to Guild Structure

If guild members are subject to significant or differential predation pressure, it should be reflected by reproductive characteristics (Martin 1988a). Predation is the primary cause of nest failure in most bird species (Cody 1971). Nest losses to predation have been reported as high as 80% for *T. major* (Brennan 2004) and almost 50% for *M. ocellata* (Gonzalez et al. 1998). Potential mammalian nest predators observed on the line-transects included coatimundi (*Nasua narica*), raccoon (*Procyon lotor*), collared peccary (*Tayassu tajacu*), white-lipped peccary (*Tayassu pecari*), and spider monkey (*Ateles geoffroyii*). Other potential mammalian nest predators occurring locally include: two large opossums (*Didelphis* spp.), nine-banded armadillo (*Dasypus novemcinctus*), ring-tailed cat (*Bassariscus sumichrasti*), and striped hog-nosed skunk (*Conepatus semistriatus*) (Garcia & Radachowsky 2003; personal observation). Although avian nest predators may be less significant for large species, corvids have been reported to be minor nest predators on *M. gallopavo* (Williams & Austin 1988). Also curassow predation on tinamou nests has been documented (Santamaria & Franco 2000). Although evidence of avian nest predation is not available locally, the study area supports diverse and abundant populations of corvids and rhamphastids (toucans).

Spatial separation of nest-sites through differential vertical or habitat placement may favor bird community diversity by mitigating predation pressure (Martin 1988a). The combination of terrestrial nest placement by *M. ocellata* and *T. major*, arboreal nest placement by *C. rubra* and *P. purpurascens*, and shrub-arboreal placement by *O. vetula* indicates vertical nest-separation within the guild. Although nest-site data collection was not systematic with

respect to habitat, there is evidence of selective habitat use within the guild. All species had significant but variable proportions of their nests in Upland forest. *C. rubra* and *P. purpurascens* nests were almost exclusively in Upland forest. *M. ocellata*, *O. vetula*, and *T. major* were the only species that nested in Scrub forest. Only *M. ocellata* and *O. vetula* exhibited substantial use of agricultural habitat.

Predation on ground nests may be greater than in other strata in tropical forests (Loiselle & Hoppes 1983; Martin 1993; Gibbs 1991). This phenomenon is supported by the relatively higher proportions of nests lost to predation by *M. ocellata* and *T. major* in this study. The perception of greater predation on ground nests in the tropics may be attributable to greater general predation pressure in the ground stratum, and therefore on terrestrial species (Martin 1988a). Gonzalez et al. (1998) reported that 40% of the *M. ocellata* hens that had successfully nested were killed by predators within 15 days of leaving the nest, and poult survival for the breeding season was only 15%. Predation on poults during the first two-weeks after hatching may represent the greatest limit to population size in *M. gallopavo* (Williams & Austin 1988).

Increased clutch sizes of some terrestrial birds are adaptive traits for conditions of high natural mortality (Martin 1988b). The significantly larger clutch sizes of *M. ocellata* and *T. major* are consistent with the prediction of greater mortality on terrestrial birds. The diversity of mating systems within the guild reflects the variation observed in clutch sizes. Curassows, guans and chachalacas not only share similar, small clutch sizes but also, as monogamous breeders, exhibit biparental care of young. *T. major* is polygynandrous; both males and females have multiple partners, but uniparental care is provided by males (Brennan 2004). *M. ocellata* is polygamous, with uniparental care provided by females. Polygynandry and polygamy, which are

life history traits consistent with high population turnover, may increase reproductive capacity or may improve population response to environmental variability, and are life history.

Relative to other general categories of birds, galliforms have lower annual survival rates and a higher rate of population turnover (Gill 1990). Although local impacts of predation on guild populations could not be directly assessed, existing evidence suggests that natural predation pressure on the guild may be significant. Potential predator species observed on the line-transects included jaguar (*Panthera onca*), puma (*Puma concolor*), ocelot (*Leopardus pardalis*), tayra (*Eira barbara*), and grey fox (*Urocyon cinereoargenteus*). Other locally occurring predators include margay (*Leopardus weidii*), jaguarundi (*Herpailurus yagouaroundi*), ornate hawk-eagle (*Spizaetus ornatus*), black hawk-eagle (*Spizaetus tyrannus*), crested eagle (*Morphnus guianensis*), and solitary eagle (*Harpyhaliaetus solitarus*) (Garcia & Radachowsky 2003, personal observation).

The only information regarding the local contribution of guild members to predator diets is from research on jaguar and puma conducted on the same study area (Novack 2003). The reported biomass proportions of “mostly cracids” were approximately 4% and 6% of jaguar and puma diet, respectively. Based on the daily caloric requirements of jaguar reported in that study, and applying a 5% correction for non-edible parts, the average jaguar or puma consumes approximately 28 kg of guild biomass annually, or the equivalent of about 8 adult *C. rubra*. Applying the density estimates for jaguar and puma from Novack (2003) to the current study area of approximately 1000 km², the local populations of these two predator species consume approximately 1,400 kg of “mostly cracids” annually. Considering that the human off-take from the guild in the study area averaged 1,625 kg of biomass annually and appeared to have a

significant impact on local populations, the natural predation pressure on the guild appears to be significant.

Alternative Influences on Guild Structure

The influence of other potentially relevant biotic factors whose impacts on the guild could not be directly assessed included resource heterogeneity, disease, and parasitism. If heterogeneity is significant to the guild, resource gradients should be diverse and species niches should have greater dimensionality. The heterogeneity of the forest habitat and the broad diet of the guild were consistent with predictions of diverse resource gradients. One potentially relevant niche dimension that was not addressed was specialized daily-activity patterns of guild members. Brooks et al. (2004) reported substantive nocturnal activity for *T. major* in a diverse tinamou community, indicating that other niche dimensions may be important to the guild. Anecdotal and circumstantial support for the potential relevance of disease comes from local reports of an historic regional crash in *M. ocellata* populations, and regional population crashes of *M. gallopavo* in North America (Williams 1981; personal observation). Parasitism may be especially relevant in tropical environments (Kricher 1997), especially for terrestrial species, which due to increased contact with the soil, often have greater parasite loads than arboreal species (Gill 1990).

Guild Response to Hunting Pressure

The recorded harvest is not representative of all subsistence hunting pressure in the study area. Although local participation in the collection effort was significant, there is no evidence that all local hunters participated or that regular participants did so all the time. In particular, harvest pressure from camp-based activities far from the village is unlikely to be well represented in the study data. During the initial stages of specimen collection, *O. vetula* and *T. major* were poorly represented. Through the deliberate efforts of some regularly participating

hunters, collection rates for *O. vetula* were increased significantly, although rates for *T. major* remained low throughout the collection period. Relative to the actual impacts of local subsistence hunting, the number of individuals harvested is expected to be slightly conservative for *C. rubra*, *M. ocellata*, *P. purpurascens*, and *T. major*, and robust for *O. vetula*. Because the proportion of sub-adult birds harvested could not be determined, the application of average adult body-mass values to the recorded harvest for each guild species probably overestimated the recorded harvest biomass. However, additional harvest pressure attributable to camp-based extraction activities (McNab 1998; Morales & Morales 1998) may compensate for any overestimation.

The harvest data indicated a disproportionately greater mean annual harvest of *C. rubra* (47%) than of other guild members, which are consistent with previously findings from the area (Morales & Morales 1998). Mean annual harvest proportions were intermediate and relatively similar for *O. vetula* (20%), *M. ocellata* (16%), and *P. purpurascens* (12%), and were consistently low for *T. major* (5%). These harvest levels were inconsistent with previous findings, which indicated that the harvest of *P. purpurascens* exceeded that of *M. ocellata* by a factor of more than 2:1, and the harvest of *M. ocellata* exceeded that of *O. vetula* by a factor of more than 5:1 (Morales & Morales 1998).

Selectivity for *C. rubra*, *M. ocellata*, and *P. purpurascens* by local hunters is consistent with population trends along the hunting gradient. Based on the changes observed in abundance estimates and guild composition between transect groups, local hunting pressure appeared to have significant impacts on populations of these three species. Although *O. vetula* and *T. major* abundance was greatest in the protected Ixcan transect group, abundance among the other three groups did not appear to be related to distance from the village of Uaxactún.

The combined population size of the guild in the heavily hunted Uaxactún South group (1,930 individuals) represented 45% of the combined guild population size in the protected Ixcan group (4,332 individuals). Estimated population sizes for Uaxactún South equated to 17% of the Ixcan population for *C. rubra*, 28% for *M. ocellata*, 89% for *O. vetula*, 31% for *P. purpurascens*, and 79% for *T. major*. Population biomass estimates were calculated using average adult body mass values and were therefore robust; however, these estimates should adequately reflect the relative differences between populations and sites. The combined biomass of the guild populations in the Uaxactún South group (3,215 kg) represented 30% of the combined biomass in the Ixcan group (10,587 kg). Based on the changes observed in the guild along the gradient, local subsistence hunting pressure has significantly reduced local guild populations.

Conclusions

Guild characteristics that were consistent with predictions of structural regulation by competitive interactions included: separation along habitat dimensions, vertical stratification, limited size assortment, and apparent competitive release by *T. major*. Guild characteristics that were inconsistent with regulation by competition included: lack of diet-niche specialization, considerable dietary overlap, limited specialization of habitat niches, and the similarity of guild membership to the regional null pool. Additional evidence contrary to regulation by competition derives from the high abundance and inter-annual increase all guild members in the protected Ixcan transect group. If the fitness of individual guild members is constrained by competitive interactions with other guild members, then it is counterintuitive that all species would exhibit greatest abundance in the same area at the same time, and that all species would exhibit abundance increases in the same area during the same time period.

Guild characteristics that were consistent with non-equilibrium processes included: limited niche specialization, limited ecological separation, and the high variability of species abundance

and habitat occupancy. Guild characteristics that were consistent with external limitations by predation included: spatial separation of nest sites and high reproductive potential of *M. ocellata* and *T. major*. Based on limited evidence of competition, evidence of non-equilibrium processes, and evidence of the importance of predation, the characteristics of the guild are most consistent with the non-equilibrium model of competition proposed by Connell (1980). The limited niche specializations and separation along resource dimensions may be sufficient to minimize direct interactions among species. The unpredictable local abundance of competitor species and external limitation of populations by predation create conditions under which dietary generalization is more adaptive than dietary specialization. Guild-member populations are unlikely to reach the carrying capacity of the environment, therefore, competitive interactions are held below levels that would lead to the competitive exclusion of potential guild members.

Table 3-1. General diet compositions of guild members based on dry-mass proportions of contents from upper-digestive tract specimens collected in Uaxactún, Flores, El Petén, from January 2000 through December 2001.

Diet compositions with all sample contents					
	<i>Crax</i> (n = 267)	<i>Meleagris</i> (n = 181)	<i>Ortalis</i> (n = 205)	<i>Penelope</i> (n = 142)	<i>Tinamus</i> (n = 55)
Flower/Stem	0.004	0.008	0.013	0.002	0.001
Animal	0.015	0.121	0.007	0.011	0.024
Leaf	0.015	0.65	0.063	0.014	0.007
Pulp	0.066	0.07	0.068	0.087	0.065
Grit	0.204	0.222	0.027	0.093	0.022
Seed	0.696	0.514	0.822	0.793	0.881
Diet compositions with grit and snail contents excluded					
	<i>Crax</i>	<i>Meleagris</i>	<i>Ortalis</i>	<i>Penelope</i>	<i>Tinamus</i>
Flower/Stem	0.005	0.012	0.013	0.002	0.001
Animal	0.016	0.011	0.006	0.012	0.024
Leaf	0.019	0.098	0.064	0.015	0.007
Pulp	0.083	0.105	0.07	0.096	0.066
Seed	0.877	0.774	0.847	0.875	0.902

Proportions include pulverized material detected in samples. The dry-mass of pulverized material was assigned to the values of separable items in each sample according to their relative proportions.

Table 3-2. Overlap of dietary seed components between species-pairs and average seed component overlap of individual species with all other guild members.

Species-pair	Seed component Overlap ^a	Species	Average Overlap ^b
<i>Crax – Meleagris</i>	57.9%	<i>Crax</i>	62.6%
<i>Crax – Penelope</i>	67.9%		
<i>Crax – Ortalis</i>	39.1%	<i>Meleagris</i>	53%
<i>Crax – Tinamus</i>	85.6%		
<i>Meleagris – Penelope</i>	57.4%	<i>Ortalis</i>	46.8%
<i>Meleagris – Ortalis</i>	32.9%		
<i>Meleagris – Tinamus</i>	63.6%	<i>Penelope</i>	66%
<i>Penelope – Ortalis</i>	65.4%		
<i>Penelope – Tinamus</i>	73.3%	<i>Tinamus</i>	68.1%
<i>Ortalis – Tinamus</i>	49.8%		

^a Calculated using equation five from Pianka (1973), pulverized material in samples was not included.

^b Average seed component overlap with all other guild members.

Table 3-3. Overlap of habitat occupancy between species-pairs and average combined overlap of individual species with all other guild members.

Species-pair	Habitat Overlap ^a	Species	Average Overlap ^b
<i>Crax – Meleagris</i>	79.5%	<i>Crax</i>	77.3%
<i>Crax – Penelope</i>	94.2%		
<i>Crax – Ortalis</i>	50.3%	<i>Meleagris</i>	82.6%
<i>Crax – Tinamus</i>	85%		
<i>Meleagris – Penelope</i>	85.4%	<i>Ortalis</i>	60.7%
<i>Meleagris – Ortalis</i>	70.8%		
<i>Meleagris – Tinamus</i>	94.5%	<i>Penelope</i>	81.7%
<i>Penelope – Ortalis</i>	56.2%		
<i>Penelope – Tinamus</i>	90.9%	<i>Tinamus</i>	83.9%
<i>Ortalis – Tinamus</i>	65.3%		

^a Calculated using proportional similarity index equation from Schoener (1970).

^b Average combined habitat occupancy overlap with all other guild members.

Table 3-4. Overlap of vertical strata occupancy between species-pairs and average combined vertical overlap of individual species with all other guild members.

Species-pair	Vertical Overlap ^a	Species	Average Overlap ^b
<i>Crax – Meleagris</i>	43.5%	<i>Crax</i>	56.4%
<i>Crax – Penelope</i>	73.8%		
<i>Crax – Ortalis</i>	68.3%	<i>Meleagris</i>	55.6%
<i>Crax – Tinamus</i>	40%		
<i>Meleagris – Penelope</i>	17.3%	<i>Ortalis</i>	41.8%
<i>Meleagris – Ortalis</i>	17.1%		
<i>Meleagris – Tinamus</i>	93.1%	<i>Penelope</i>	43.3%
<i>Penelope – Ortalis</i>	68.3%		
<i>Penelope – Tinamus</i>	13.8%	<i>Tinamus</i>	40.1%
<i>Ortalis – Tinamus</i>	13.6%		

^a Calculated using proportional similarity index equation from Schoener (1970).

^b Average combined vertical overlap in both forest-classes with all other guild members.

Table 3-5. Density estimates for *Crax rubra*, *Meleagris ocellata*, *Ortalis vetula*, *Penelope purpurascens*, and *Tinamus major* by forest-class in the Maya Biosphere Reserve, Guatemala.

Transect group	Ixcán	Ixcán	Cedro	Cedro	Uaxactún North	Uaxactún South
Sampling period	2000-2001	2001-2002	2000-2001	2001-2002	2000-2001	2000-2001
Upland forest densities (km ²)						
<i>Crax</i>	31.19	31.05	21.37	26.27	14.44	5.46
<i>Meleagris</i>	15.51	24.63	6.44	16.7	8.04	4.7
<i>Ortalis</i>	11.25	12.56	14.51	22.91	3.37	18.51
<i>Penelope</i>	24.31	28.29	16.43	15.78	7.27	6.73
<i>Tinamus</i>	8.44	14.64	5.46	5.16	10.96	9.13
Scrub forest densities (km ²)						
<i>Crax</i>	14.17	19.54	6.12	9.94	6.18	2.42
<i>Meleagris</i>	15.19	17.41	3.4	22.73	7.87	5.2
<i>Ortalis</i>	37.22	56.03	24.19	25.29	19.03	25.01
<i>Penelope</i>	11.11	15.81	6.12	6.28	4.56	6.32
<i>Tinamus</i>	10.37	8.97	6.8	6.54	6.39	4.51

Density estimates calculated using DISTANCE version 5, release "Beta 5".

Table 3-6. Guild compositions based on proportional population size and relative biomass at each transect group.

Transect group	Ixcán	Ixcán	Cedro	Cedro	Uaxactún North	Uaxactún South
Sampling period	2000-2001	2001-2002	2000-2001	2001-2002	2000-2001	2000-2001
Proportional population size						
<i>Crax</i>	0.28	0.24	0.317	0.289	0.236	0.106
<i>Meleagris</i>	0.172	0.167	0.098	0.197	0.181	0.109
<i>Ortalis</i>	0.227	0.247	0.248	0.264	0.25	0.455
<i>Penelope</i>	0.219	0.213	0.246	0.168	0.135	0.15
<i>Tinamus</i>	0.102	0.133	0.091	0.082	0.198	0.18
Proportional population biomass						
<i>Crax</i>	0.391	0.351	0.464	0.399	0.355	0.216
<i>Meleagris</i>	0.294	0.302	0.177	0.336	0.334	0.274
<i>Ortalis</i>	0.059	0.068	0.068	0.069	0.071	0.175
<i>Penelope</i>	0.207	0.212	0.245	0.157	0.138	0.208
<i>Tinamus</i>	0.049	0.067	0.046	0.039	0.102	0.127

Population sizes were based on density estimates by forest-class extrapolated by the availability of each forest-class within the 50km² area corresponding to each transect group. Population biomass estimates were based on population size and average adult body mass of each species.

Table 3-7. Temporal reproductive patterns of *Crax rubra*, *Meleagris ocellata*, *Ortalis vetula*, *Penelope purpurascens*, and *Tinamus major* based on the number of monthly observations of reproductive activities.

Category	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.
<i>Crax rubra</i>												
Calls	8	14	38	36	46	30	8	4				1
Nests				8	1	5						
Young				2	5	7	10	1	1	2		
<i>Meleagris ocellata</i>												
Calls		1	21	43	38	2	1					
Nests				3	9	4						
Young			1	1	4	1	2		2	2		
<i>Ortalis vetula</i>												
Nests			1	7	30	31						
Young			3	5	7	5	3	3		1		
<i>Penelope purpurascens</i>												
Nests				3	3	4	3					
Young					3	5	8		1			
<i>Tinamus major</i>												
Nests			1		6	9	12	1	1			
Young				2		3	6	8	3			

Calls include records of vocalizations specific to reproductive behavior which were recorded only for *C. rubra* and *M. ocellata*. Nests include only observations of nests with laying or incubating adults present. Young include observations of dependent young and hatched nests observed during the nesting period.

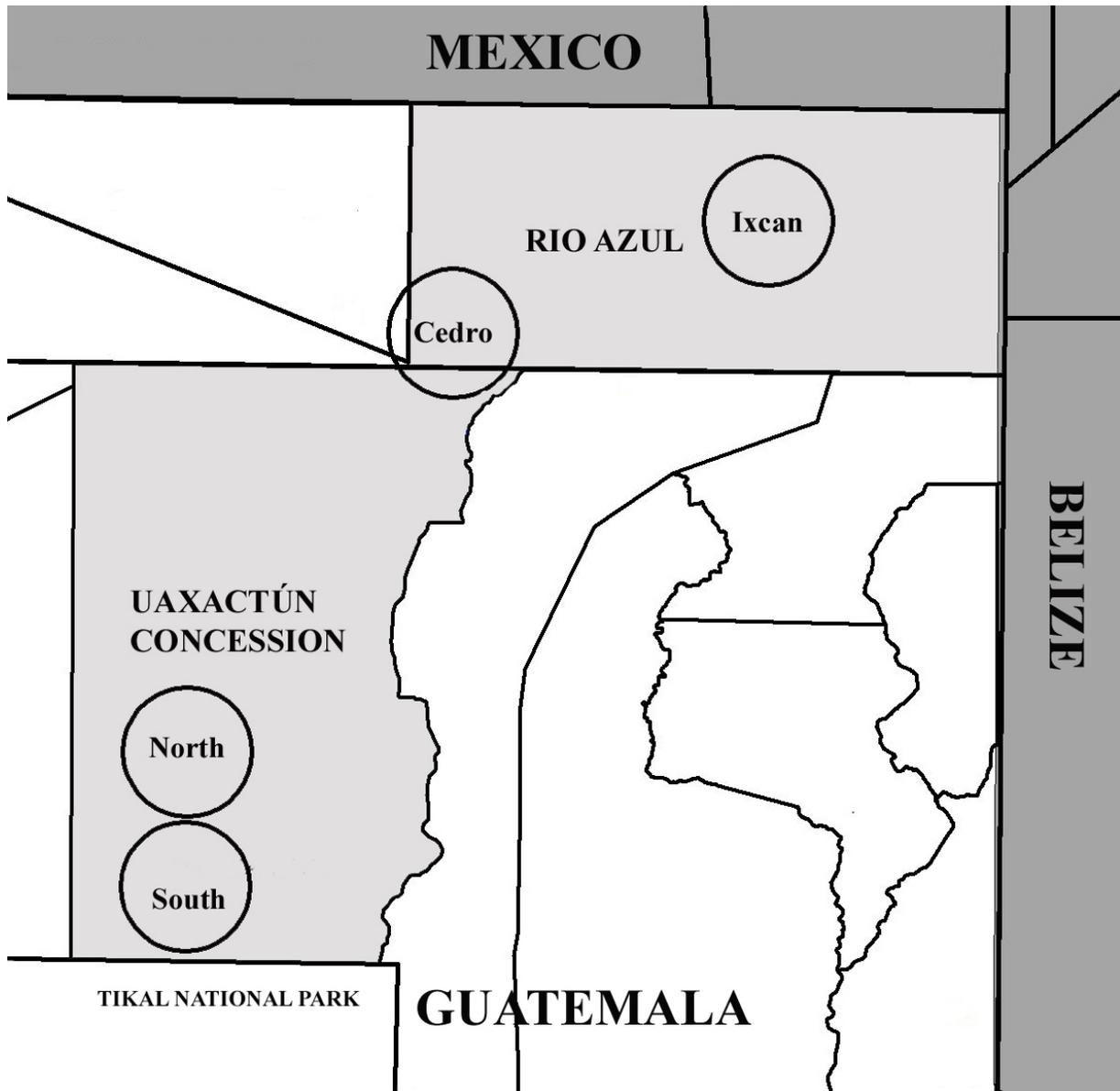


Figure 1-1. Map of study area. Lightly shaded areas indicate the two management units in which study data were collected. Circles depict the 50km² areas corresponding to each transect group.

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BIOGRAPHICAL SKETCH

At his point I have lived roughly equal proportions of my life in Texas, New Jersey, and Guatemala. I received a B. S. in zoology and another in wildlife management from Texas Tech University in Lubbock, Texas. After graduating from Texas Tech I entered the U. S. Peace Corps and was stationed in Guatemala where I worked with non-governmental organizations working in the two largest protected areas in that nation, first in the Sierra de las Minas Biosphere Reserve and later in the Maya Biosphere Reserve. My interests in terrestrial vertebrate ecology and sustainable wildlife resource-use lead me to pursue graduate studies at the Department of Wildlife Ecology and Conservation at the University of Florida. Since 1999 I have co-developed and managed the Guatemalan operations of a community-based, sport-hunting, conservation project for the Ocellated Turkey working in community forestry concessions in the multiple-use zone of the Maya Biosphere Reserve.