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Pablo Rafael Bolanos Sittler

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Pablo BOLAÑOS

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**Acoustic behavior and ecology of the Resplendent Quetzal
Pharomachrus mocinno, a flagship tropical bird species**

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THE PRIMORDIAL WORLD

This is the account of when all is still silent and placid. All is silent and calm. Hushed and empty is the womb of the sky. These, then, are the first words, the first speech. There is not yet one person, one animal, bird, fish, crab, tree, rock, hollow, canyon, meadow, or forest. All alone the sky exists. The face of the earth has not yet appeared. Alone lies the expanse of the sea, along with the womb of all the sky.

There is not yet anything gathered together. All is at rest. Nothing stirs. All is languid, at rest in the sky. There is not yet anything standing erect. Only the expanse of the water, only the tranquil sea lies alone. There is not yet anything that might exist. All lies placid and silent in the darkness, in the night. All alone are the Framer and the Shaper, Sovereign and Quetzal Serpent, They Who Have Borne Children and They Who Have Begotten Sons. Luminous they are in the water, wrapped in quetzal feathers and cotinga feathers. Thus they are called Quetzal Serpent. In their essence, they are great sages, great possessors of knowledge. Thus surely there is the sky. There is also Heart of Sky, which is said to be the name of the god.

(A fragment of the Mayan sacred book Popol Vuh, translation by A. Christenson)



(Picture: Pablo Bolaños)

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Résumé



Volcanoes around the Atitlán lake, Guatemala, from left to right: Atitlán, Tolimán and San Pedro (Picture: Pablo Bolaños)

Comportement et écologie acoustiques du Quetzal Resplendissant *Pharomachrus mocinno*, une espèce porte drapeau d'oiseau tropical.

Le Quetzal Resplendissant *Pharomachrus mocinno* est une espèce d'oiseau tropical dont les populations sont fortement menacées, notamment au Guatemala. Son commerce est réglementé au niveau international et l'espèce est incluse dans la liste rouge des espèces menacées de l'Union Internationale pour la Conservation de la Nature (UICN). La réduction de son habitat, la forêt de nuage, due aux activités humaines comme l'agriculture et le trafic de spécimens et de plumes sont les principales raisons du déclin des populations. Le Quetzal Resplendissant joue un rôle important de disperseur de graines, les adultes étant strictement frugivores. Par ailleurs, l'espèce constitue le centre de la culture maya passée et présente, surtout au Guatemala, où elle est considérée comme le plus important symbole national. Il existe deux sous-espèces connues du genre *Pharomachrus* : *P. m. mocinno* (nord de l'Amérique centrale et sud du Mexique) et *P. m. costaricensis* (sud de l'Amérique centrale). Néanmoins, selon des études morphométriques et génétiques, les deux sous-espèces pourraient être considérées comme des espèces valides.

Les études disponibles sur le Quetzal Resplendissant recouvrent plusieurs aspects de son histoire naturelle et de sa biologie. Néanmoins, il n'y avait à ce jour aucune description du répertoire acoustique, pourtant nécessaire pour mieux comprendre le comportement et l'écologie de l'espèce. L'objectif général de cette thèse a été d'étudier le comportement et l'écologie acoustiques du Quetzal Resplendissant dans la forêt de nuage du Guatemala. Plus particulièrement, il s'agissait de développer quatre axes de recherches principaux. Le premier axe consistait à décrire le répertoire vocal à partir d'observations directes dans des réserves naturelles de forêt nuageuse. Le second axe avait pour but de rechercher s'il existait des différences de structure entre les vocalisations des sous-espèces de *P. mocinno*. Le troisième axe consistait à savoir s'il était possible de suivre les populations de Quetzal Resplendissant à partir d'un système acoustique automatique. Enfin, le quatrième axe considérait la compétition acoustique interspécifique entre le Quetzal Resplendissant et les autres espèces appartenant à la même communauté acoustique.

Les vocalisations de *P. mocinno* ont été décrites quantitativement et précisément en temps et en fréquence pour la première fois. L'observation des individus *in situ* et une analyse détaillée des vocalisations, y compris des expériences de propagation de

ces vocalisations dans l'habitat naturel, ont permis d'identifier quatre types de vocalisations : les signaux territoriaux, de cour, d'alarme, et de contact. Les expériences de propagation ont montré que les vocalisations de territoire et d'alarme possèdent des propriétés acoustiques adaptées à la communication à longue distance, tandis que celles de cour et de contact ont des caractéristiques typiques de signaux fonctionnant à courte distance.

Une fois les vocalisations de *P. m. mocinno* répertoriées et décrites, il était possible d'estimer les différences potentielles entre les vocalisations des deux sous-espèces afin de tester les hypothèses de différenciation spécifique. Pour cela, des analyses multivariées ont été entreprises afin de comparer les vocalisations territoriales non seulement des deux sous-espèces mais aussi de comparer les vocalisations territoriales de *P. m. mocino* avec celles d'autres espèces du genre *Pharomachrus*, à savoir *P. antisianus*, *P. auriceps*, *P. pavoninus*, *P. fulgidus*. Une analyse de classification supervisée par la méthode de Random Forest ainsi qu'une analyse en composantes principales ont révélé des différences significatives entre les sous-espèces. Entre autres, la fréquence des vocalisations territoriales de *P. m. mocinno* est plus élevée que celle observée chez *P. m. costaricensis*, sous-espèce plus petite en taille. Cette observation va à l'encontre de la règle générale qui stipule que la fréquence émise est négativement corrélée avec la taille du corps. Ces résultats soutiennent l'hypothèse que les deux sous-espèces devraient être considérées comme deux espèces valides. Une telle distinction a des conséquences importantes pour la conservation et les politiques de protection de ces oiseaux charismatiques. En effet, le niveau spécifique réduit le nombre de populations et l'aire géographique occupée par chaque taxon, augmentant de fait, le risque d'extinction. Espèces porte drapeau au niveau national, mais aussi international, leur conservation a également des conséquences sur la conservation plus globale de leur habitat, la forêt de nuage, environnement particulièrement sensible aux changements climatiques. Ces résultats revêtent donc une importance capitale pour la protection des espaces naturels d'Amérique Centrale.

L'UICN suppose que les populations du Quetzal Resplendissant sont en diminution, mais il n'existe pas de données quantitatives, principalement en raison de l'absence de méthodes efficaces de suivi des populations. La couleur et le comportement cryptiques de cet oiseau rendent difficile la détection des individus dans

le milieu dense et complexe de leur habitat. Qui plus est, le comportement de *P. mocinno* peut être affecté par la présence d'observateurs humains et les méthodes actuelles de suivi (télémétrie, géotracking) nécessitent la capture et la manipulation des individus, interventions fortement controversées en raison de la grande importance écologique et culturelle de l'espèce. Un système acoustique automatique a donc été mis au point pour détecter et suivre l'espèce de manière efficace et non invasive. Le système, reposant sur la méthode de reconnaissance par corrélation croisée, a été développé et validé à partir d'annotations manuelles. Le système s'est avéré efficace (85% de détections correctes), pouvant être ensuite appliqué aux enregistrements obtenus au moyen de quatre enregistreurs fonctionnant pendant deux semaines au cours du mois de février (début de la saison de reproduction du *P. mocinno*) en 2016 et 2017. L'influence possible de facteurs environnementaux sur le nombre de détections obtenues a été analysée à l'aide d'un modèle linéaire généralisé mixte. Les résultats ont révélé des quantités de détections liées à certaines variables environnementales. En particulier, lorsque la nébulosité est élevée, le nombre de détections automatiques de *P. mocinno* est supérieur à celui observé pour les périodes peu nuageuses.

Enfin, la communauté acoustique des oiseaux à laquelle appartient *P. mocinno* a été analysée au moyen d'une nouvelle méthode. Premièrement, les espèces partageant la même bande de fréquences que *P. mocinno* ont été identifiées. Deuxièmement, le chevauchement potentiel dans le temps et la fréquence entre les vocalisations de *P. mocinno* et celles d'autres espèces partageant le même habitat a été ensuite quantifié. Enfin le chevauchement acoustique potentiel de chaque espèce a été comparé au chevauchement acoustique réel observé. Afin de pouvoir visualiser la compétition entre chaque espèce de la communauté et *P. mocinno* une analyse en composantes principales a été réalisée. Les facteurs pris en considération étaient non seulement le chevauchement acoustique entre les espèces de la communauté et *P. mocinno* (compétition acoustique), mais également d'autres facteurs de compétition, tels que les ressources alimentaires, le type de nid ou la prédation. La distance phylogénétique des espèces avec *P. mocinno* a également été prise en compte. Les résultats ont révélé des patrons de compétition. En général, le chevauchement acoustique entre *P. mocinno* et les autres espèces de la communauté acoustique était élevé avec les espèces en compétition pour les ressources alimentaires et faible avec les espèces prédatrices de

P. mocinno. Le principal compétiteur de *P. mocinno* était *Trogon mexicanus*, une espèce étroitement apparentée phylogénétiquement.

A partir de nouvelles méthodologies acoustiques, il a donc été possible de proposer une première description des vocalisations de *P. mocinno*, de suggérer une révision taxonomique ayant des conséquences importantes sur la politique de conservation, de mettre au point d'un système de surveillance acoustique automatique de l'espèce et de proposer pour la première fois une analyse des interactions au sein d'une communauté acoustique. L'approche développée pourrait être appliquée sur la même espèce sur différents sites, mais également sur d'autres espèces. La bioacoustique et l'écoacoustique apparaissent donc comme des disciplines de grand intérêt pour l'étude comportementale et écologique d'espèces d'intérêts majeurs.

General Introduction



Resplendent Quetzal (Picture: Ricky Lopez)

Conservation in terrestrial environments

Biodiversity loss is increasing every year mostly due to human activities (DeClerck et al, 2010). Establishment of protected areas is one of the most widely used tools for biodiversity conservation (Rayn & Sutherland, 2011), protecting areas covering about 12% of the land surface (Chape et al, 2008). In theory a protected area can inhibit deforestation through a variety of mechanisms: a) protecting natural resources that would otherwise be exploited, b) preventing or mitigating the effects of investments in roads and other infrastructure that cause direct environmental damages and/or indirectly foster natural resource exploitation, or c) preventing agricultural settlements (Nepstad et al, 2006). Nevertheless the management needs of protected areas varies between them, and much of the conservation literature and policy recommendations are directed at protected areas that are uninhabited (Castillo & Toledo, 2000). In order to take well based management decisions for conservation, it is necessary to generate evidence about the status of the ecosystems (Sutherland et al, 2004). The task of generating information about ecosystem status is increasingly difficult in complex environments such as tropical forest, where many species still remain unknown (Eldridge et al, 2016). The management of ecosystems is a challenging task being even more difficult in the Third World, where approximately 95% of the agricultural population occurs (Castillo & Toledo, 2000), having an important impact on forest fragmentation.

Conservation in the tropics

About 44% of all species of vascular plants and 35% of all species of vertebrates are confined to 25 hotspots covering only 1.4% of the land surface on Earth, and most of these hotspots are located in the tropical region, where one of the most biodiverse ecosystems are located in Mesoamerica (Myers et al, 2000), the area occupied by the Mayan civilization. Mesoamerica is both a land bridge between two major continents and a barrier between two major oceans (DeClerck et al, 2010). The joining of North America and South America about three million years ago facilitated the Great American Biotic Interchange, which is determinant in the configuration of the current American biota (Pelegrin et al, 2018). Mesoamerica is considered one of the original 25 global biodiversity hotspots (Myers et al, 2000). The region is narrow (80 km at its narrowest), bordered by the Pacific Ocean to the West and the Caribbean Sea to the East, and divided by a volcanically active central mountain range reaching elevations of 4220 m on Tajumulco volcano in Guatemala, and 3820 m on Chirripó in Costa Rica. Both the oceans and mountain range that divides them influence the distribution of

four terrestrial biomes and 19 terrestrial ecoregions in Mesoamerica (Estado de la Región 2006).

Cloud forest

Some forests in tropical areas are characterized by a high humidity rate, the cloud forest is one of these, which occurs in the middle-to high-altitude range (Figure 1). Cloud forests need a high humidity and an elevation typically higher than 1000 m (Eisermann & Avendaño 2008). This habitat type is distinct to other forests in that a substantial portion (up to nine percent) of the water input comes from interception of moisture of clouds as they move through the forest (Ataroff & Rada 2000; Holder 2004), and support a rich abundance of epiphytes (Chape et al, 2008). In the humid tropics the bases of mountains are dominated by lower montane rainforest, followed in ascending order by montane rainforest and then upper montane rainforest. This may merge into the montane cloud forest, where there are persistent clouds. The need upon clouds to supply the cloud forest with atmospheric moisture makes it especially vulnerable to climate change (Chape et al, 2008). Research has shown that the mean cloud base is moving upwards on tropical mountains as a result of climatic shifts. The forest species are not able to migrate a comparable rate and, in any case, range shifts will be limited by the land area existing at higher elevations (Pounds et al, 1999a).

The cloud forests in the Neotropics are distributed between 23° of north latitude and 25° of south latitude, at an altitudinal range between 1000 and 3000 m.a.s.l. (Webster, 1995). As in other tropical regions, in the Neotropics, climate change and changes in the land use has been the cause of local extinctions (Chape et al, 2008). Climatic fluctuations have been also responsible for extinctions of restricted species to cloud forest (Pounds et al, 1999b). Furthermore, as cloud forests are converted to agricultural land, an altitudinal frontier has emerged in montane environments in Latin America (Ataroff & Rada 2000, Pope & Harbor 2014, Holder 2004). The lower parts of the mountains and volcanoes have suffered a stronger impact of deforestation than the higher parts (Pope & Harbor, 2014), these changes in land use can have profound impacts on water resources (Holder 2004). Habitat fragmentation modifies the microclimatic conditions of the adjacent forests, incrementing wind, sunlight and rain expositions (Didham & Lawton 1999). Furthermore, fragmentation of lower parts of the mountains can affect altitudinal migrations of threatened bird species, like the Resplendent Quetzal (Hsiung et al, 2018; Powell & Bjork, 1995).



Figure 1: Representative cloud forest present in the south slope of Volcano Atitlán, Guatemala (Photo: Pablo Bolaños)

Cloud Forest in Guatemala

In Guatemala the cloud forest is distributed along the volcanic chain and mountains that meet the necessary weather conditions. The cloud forest in Guatemala, as in other parts of its world distribution is a biodiversity rich habitat, supporting symbolic species of animals like the Resplendent Quetzal *Pharomachrus mocinno*, and plants like the orchid *Lykaste skinner*, respectively the national bird and flower of Guatemala. The Atitlan volcano is an important remnant of cloud forest in Guatemala. The area is located in a zone of high endemism of bird species (Eisermann & Avendaño, 2008). The forest of the Atitlan volcano is typical of the volcanic chain of Guatemala, with broadleaved cloud forest in elevated areas and moist broadleaved forest in lowland areas. The south slope of the Atitlan volcano receives a precipitation average of 4,500 mm a year, this precipitation decreases drastically (1089 mm) on the north slope of the volcano. The south face of the volcano has slopes up to 30°, the soil is 35% sandy, 65% clayey, with abundant organic material. Typical tree forest species are *Quercus skinneri*, *Q. corrugata*, *Sloanea ampla*, *Brosimum guianense*, *Oreopanax xalapensis*, *Sterculia Mexicana*, *Olmediella betschleriana*, *Xylosma flexuosum* and *Trophis*

chiapensis. The forest has abundant epiphytes of the family Bromeliaceae and a high diversity of Orchideaceae. The undergrowth is dominated by a high diversity of plants of the family Rubiaceae, like *Psychotria* spp. and *Hoffmania* spp., also arborescent ferns of the genus *Cyathea*, and terrestrial ferns of *Polypodium* spp. (Dix et al, 2003). The forest present in “Refugio del Quetzal” in the department of San Marcos is another fragment of cloud forest occurring in an area important area for its endemics (Eisermann & Avendaño, 2008).

Avifauna of the cloud forest

Mesoamerican cloud forests contain 228 of the 2534 bird species restricted to cloud forests around the world (Long, 1995), and a high quantity of species are greatly threatened (Islebe & Véliz Pérez, 2001). Many Endemic Bird Areas are located within cloud forests, consequently are threatened by human activities that are having an impact on the habitat (Renner, 2003).

Tropical montane cloud forests are located between 500 and 3500 m.a.s.l. (Renner, 2003). In the southern slope of the Atitlan volcano, the cloud forest is located approximately between 1300 and 2500 m.a.s.l. (Dix et al, 2003).

The Mesoamerican cloud forest is an important hotspot of endemism (Myers et al, 2000). Characteristic bird species of the Mesoamerican cloud forest are the Resplendent Quetzal (*P. mocinno*), Slate colored Solitaire (*Myadestes unicolor*), Green Toucanet (*Aulacorhynchus prasinus*), Mountain Trogon (*Trogon mexicanus*) or the Slate-throated Redstart (*Myioborus miniatus*). Bird species endemic to the cloud forest habitat of Mesoamerica, are the Blue Throated Mot-Mot (*Aspatha gularis*), Horned Guan (*Oreophasis derbianus*), Pink-headed Warbler (*Cardellina versicolor*), Rufous-browed Wren (*Troglodytes rufociliatus*), Green-throated Mountain-gem (*Lampornis viridipallens*), Highland Guan (*Penelopina nigra*) and Fulvous Owl (*Strix fulvescens*). Other species like the Brown-backed Solitaire (*Myadestes occidentalis*), Black-capped Swallow (*Notiochelidon piliata*), Rufous-collared Robin (*Turdus rufitorques*), Sharp-shinned Hawk (*Accipiter striatus chionogaster*), Bushy-crested Jay (*Cyanocorax melanocyaneus*), Cabanis Tanager (*Tangara cabanisi*), Blue-and-white Mockingbird (*Melanotis hypoleucus*), Black-capped Siskin (*Carduelis atriceps*) or Wine-throated Hummingbird (*Atthis ellioti*), are endemic to northern Central American highlands but not restricted to cloud forest habitat (IARNA/URL, 2008).

Some of the species distributed in most of the area covered by cloud forests in Guatemala are the Rufous-browed Wren (*Troglodytes rufociliatus*), Gray-breasted Wood-Wren (*Henicorhina leucophrys*), Ruddy-capped Nightingale-Thrush (*Catharus frantzii*), Golden-browed Warbler (*Basileuterus belli*), and Common Bush- Tanager

(*Chlorospingus ophthalmicus*). It has been suggested that the cloud forest avifauna of northern Central America (eastern Chiapas, Guatemala, El Salvador and Honduras) is similar, although some differences has been reported (Eisermann & Schulz, 2005).

Along its area of occurrence, the cloud forest is highly fragmented. This implies a loss of connectivity between some bird populations of the different forest fragments, depending on their flying capacity. There are some differences in the composition of bird species in the cloud forest remnants of Guatemala (Eisermann & Schulz, 2005). The difference could be greater between fragments with low connectivity. In the case of *P. mocinno*, the cloud forest of Sierra de las Minas, the largest cloud forest of Guatemala, is located at an approximate distance of 35 km from the cloud forest of Caquipec, separated by the Polochic valley. Here, interchange between Resplendent Quetzal populations of both sites has been reported. Radio tagged individuals apparently moved from the Sierra de las Minas to the Sierra de Chuacús forest, and then to Yalijux and Caquipec (Paiz, 1996). In another study (Yurrita, 2013), there were registered movements of *P. mocinno* between the forest of Cerro Verde and the separated forest of Biotopo del Quetzal, and the distance of the movements registered did not exceed 5.34 km.

Species Description

Pharomachrus genus

The species *P. mocinno* belongs to the order Trogoniformes (Trogons and Quetzals), which includes a single family Trogonidae. This family is one of the most remarkable bird groups mostly due to the brightly colored plumage. In addition, the species of trogonids are good seed dispersers, and have been used as indicators for protected areas design (Powell & Bjork, 1995).

General introduction

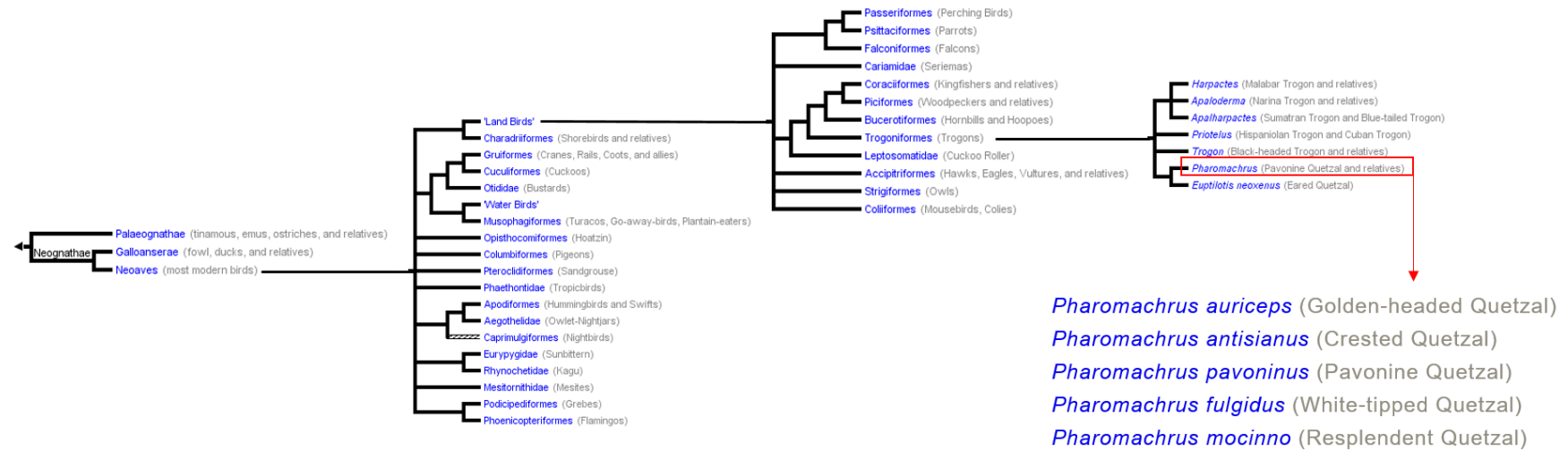


Figure 2: Position of *Pharomachrus* genus in the taxonomic tree of the clade Neoaves (Modern birds) (Tree of Life Web Project, 1999)

The order Trogoniformes includes seven genera, most of the extant species are distributed in the New World (25 species) and the rest occurring in Africa and Asia (14 species). Species richness among trogonids is greatest in Central and South America (Johnsgard, 2000). Figure 2 shows the phylogenetic position of Trogoniformes among the other orders of the clade Neoaves. The phylogenetically closest bird groups to the order Trogoniformes are the orders Bucerotiformes (Hornbills and Hoopoes), the Piciformes (Woodpeckers, Toucans and relatives) the Coraciiformes (Kingfishers and relatives), the members of the family Leptosomatidae (Cuckoo Roller), the orders Accipitriformes (Hawks, Eagles, Vultures and relatives), the Strigiformes (Owls) and the order Coliiformes (Mousebirds, Colies). Then, the genus *Pharomachrus* is phylogenetically closer to the genus *Euptilotis*, with only one species *Euptilotis neoxenus* (Eared Quetzal), and the genus *Trogon* (Black-Headed Trogon and relatives). The genus *Pharomachrus* has five recognized species, *P. pavoninus* (Spix 1924), *P. mocinno* (De la llave 1832), *P. antisianus* (d'Obigny 1837), *P. fulgidus* (Gould 1838) and *P. auriceps* (Gould 1842). Figure 3 shows the species diversity of trogons by latitudinal zones in the Old World and New World. There is a gradient in the number of species, being more abundant between 0° and 15° of latitude.

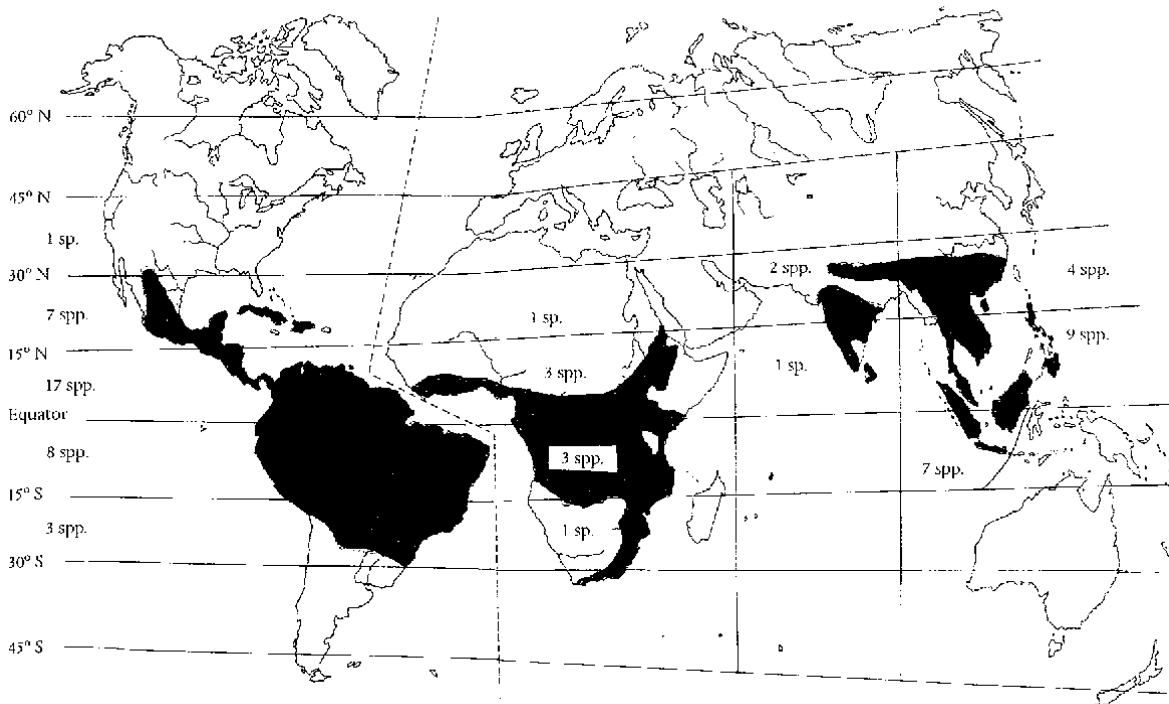


Figure 3 : Species diversity of Trogons by latitudinal zones in the Old World and New World. Obscure areas show approximate collective limits of trogon ranges in each region (diagram: Johnsgard, 2000)

The order Trogoniformes, and its unique family Trogonidae, is characterized by a heterodactyl toe arrangement, in which both the first (hind) and second (normally inner front) toes are oriented posteriorly, and the third and fourth toes are oriented to the front (Figure 4). This arrangement of the toes differentiates the family Trogonidae from the other bird groups. The heterodactyl arrangement, could be an adaptation to cling to the sides of rotted trees as they excavate trunk cavities. Walking and hopping are rare, due to the relatively small size of their feet and legs (Johnsgard, 2000).

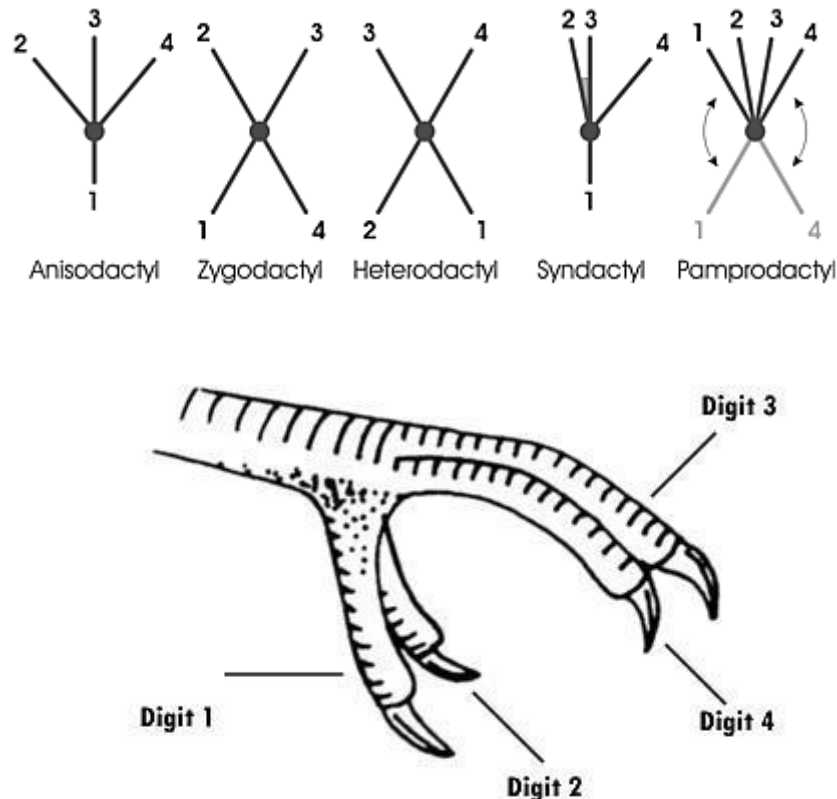


Figure 4: Toe arrangements among birds. The heterodactyl arrangement is exclusive of the order Trogoniformes, the first (hind) and second (normally inner front) toes are oriented posteriorly, so that two toes (the third and fourth) are oriented to the front (source: Wikimedia)

It has been suggested that the ancestral origin of trogonids was Africa and that they later invaded Asia and, more recently, the Neotropics (Espinosa de los Monteros, 1998), nevertheless latter studies did not find significant support to this hypothesis, suggesting that the ancestral origin for modern trogons is the Neotropics (Moyle, 2005). The family Trogonidae includes seven genera: *Harpactes* (Malabar Trogon and relatives) distributed in tropical Asia; *Apaloderma* (Narina Trogon and relatives) in Africa; *Apalharpactes* (Sumatran Trogon and Blue-tailed Trogon) restricted to the Indonesian islands of Java

and Sumatra; *Priotelus* (Hispaniolan Trogon and Cuban Trogon) distributed in the Neotropics; *Trogon* (Black-headed Trogon and Relatives) in subtropical to tropical areas in America, Southeast Asia and the Greater Sunda Islands; *Euptilotis* (Eared Quetzal) in Southwest Arizona and Mexico and *Pharomachrus* (Resplendent Quetzal and relatives) distributed from South Mexico to north Peru and Brazil (Johnsgard, 2000).

The genus *Pharomachrus* differentiates from the others of its tribe in that the maxilla does not present serrations on its edges, and that the nostrils are narrow and mostly hidden by the operculum. The *Pharomachrus* species have brushy antrose feathers on the forehead, the lores, and chin superpose to the base of the bill. The median wing-coverts are elongated and highly iridescent, decurved, and pointed. In adult males the four middle upper tail-cover feathers are greatly elongated, pointed and also highly iridescent. These elongated feathers are much more developed in males than females and immature males (Johnsgard, 2000). In all the species of the genus *Pharomachrus*, nearly all the green feathers are iridescent green to golden green, and the underparts are entirely or partly red. The red color is caused by the carotenoid pigment zooerythrine. Conversely iridescent green color is not produced by pigmentation, in contrast the feathers present parallel rows of melanin granules, spaced at approximately 5400 Å apart, approximately the wavelength of green light. Thus the feathers reflect green, by the physical phenomenon of interference (LaBastille et al, 1972). The five species of the genus are mainly frugivorous (Johnsgard, 2000). Figure 5 shows the external morphology of trogons, showing locations of some anatomical and structural terms mentioned in the descriptions.

Pharomachrus mocinno

The most notorious morphological character that separates *P. mocinno* from the other species of its genus is the elongated upper-tail cover feathers of males (Fagan & Komar, 2016). *Pharomachrus mocinno* has two recognized subspecies, *P. m. mocinno* occurring in the cloud forest from South Mexico to north Nicaragua, and *P. m. costaricensis* in Costa Rica and Panama (Solórzano & Oyama, 2009). Figure 6 shows the distribution of *P. m. mocinno* and *P. m. costaricensis*.

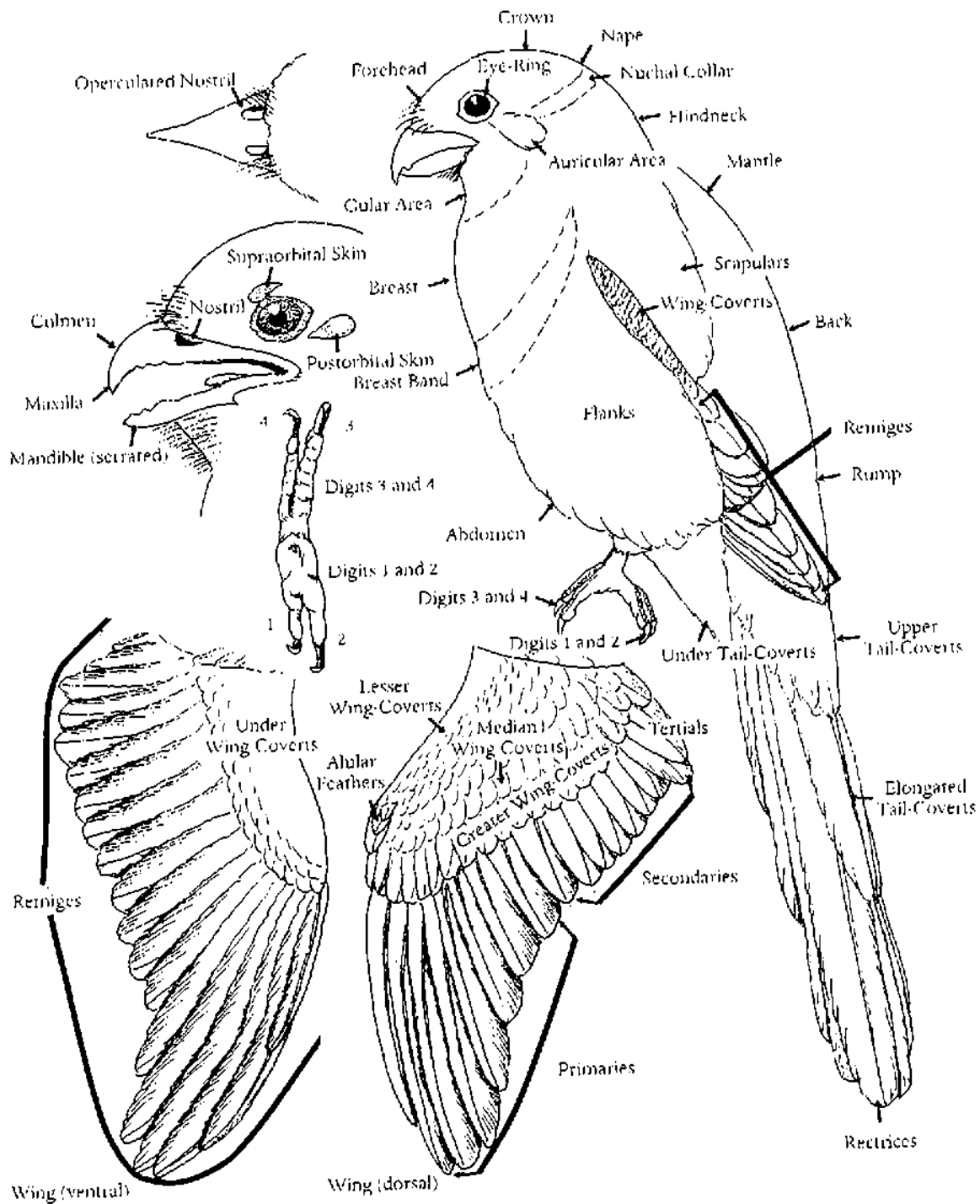


Figure 5: External morphology of trogons, showing locations of some anatomical and structural terms mentioned in the descriptions (diagram: Johnsgard, 2000)

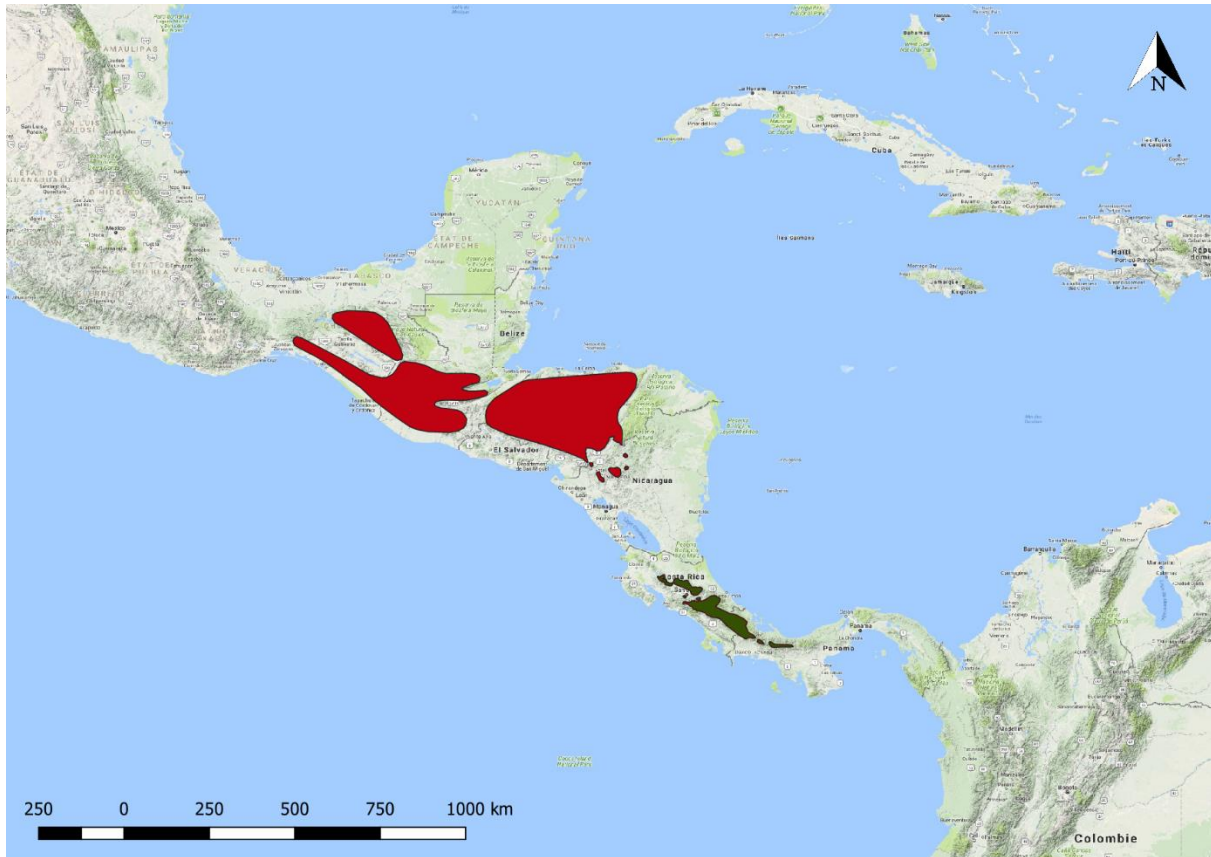


Figure 6: Distribution of *P. m. mocinno* (red) and *P. m. costaricensis* (green) (Birdlife 2016)

Morphological description

Adult Male:

As described by Johnsgard (2000): “Upperparts, head, neck, and chest brilliant iridescent green or golden green, changing to bluish green or greenish blue depending on light angle; elongated greater wing-coverts with basal portion abruptly black; greater secondary and primary wing-coverts, alular feathers, and six middle rectrices uniform black; three outer rectrices white with black shaft, basal portion greyish black or slate; underparts posterior to chest intense carotenoid red, darkening to crimson or burnt carmine on upper breast; thigh feathers black, lower ones glossed with iridescent green; bill yellow to orange-yellow; iris dark brown; feet and toes olive to dull orange brown”. In Figure 7 a photograph of an adult male of *P. m. mocinno* is shown.

Adult Female:

“Crown and sides of head iridescent bronze-green, the cheek and laterofrontal feathers much less developed than those in male; back, scapulars, wing-coverts, rump, and upper tail-coverts not reaching far, if at all, beyond tip of tail; remiges black, primaries broadly edged with buff; tail black, three outer rectrices on each side broadly white distally and

on outer vanes, white portion with dusky barring; chin and throat greyish brown; extreme lower abdomen, rear flanks, vent region, and under tail-coverts pure carotenoid red; thighs sooty blackish, the lower feathers glossed with iridescent green; maxilla blackish, streaked with yellow, sometimes entirely yellow; mandible dull yellow, tinged with green toward base; iris dark brown; feet and toes dull green to olive-brown” (Johnsgard, 2000). Figure 8 shows an adult female of *P. m. mocinno*.



Figure 7: *Pharomachrus mocinno mocinno*, adult male, taken at Refugio del Quetzal, San Marcos, Guatemala in 2017 (Picture: Pablo Bolaños)

Immature Male:

“Similar to adult female, but iridescent green of head and upperparts brighter; breast, abdomen, and sides grey instead of greyish brown; distal portion of rectrices broadly barred with white, outer rectrices barred only near base and more pointed than in adult; buff edges of outer vanes of primaries toothed with black; outer vanes of secondaries intermixed with buff; bill yellowish; other soft-part colours as in adult” (Johnsgard, 2000).

Juvenile:

The juveniles are brown above, the scapulars and wing-coverts are mottled. The wing feathers have buffy edges. The breast is cinnamon coloured and edged with greyish brown. The lower breast and abdomen are white, with greyish brown on the sides. The middle rectrices are brownish black and the outer ones are white (Wetmore, 1967). Approximately two weeks after hatching, some green iridescence may appear on the contour feathers and wing-coverts; two to three days after, green-tipped feathers can appear on the neck and scapulars, the iris is brown, the feet are lead coloured and the bill is black (Wheelwright, 1983). The bills of nestlings with eyes still closed, are blackish only near the middle, with yellowish tips and base (Bowes 1969).



Figure 8: *Pharomachrus mocinno mocinno*, adult female, taken at Refugio del Quetzal, San Marcos, Guatemala in 2017 (Picture: Pablo Bolaños)

***Pharomachrus mocinno* subspecies**

Two subspecies have been recognized, separated by the lowlands of Nicaragua, *P. m. mocinno* from south of Mexico to north of Nicaragua, and *P. m. costaricensis*, in Costa Rica and Panama. *Pharomachrus mocinno* was first described by Pablo de la Llave from

a specimen collected in Guatemala (“Goatemala”) (1832). Later, in 1869, Jean Louis Cabanis classified specimens collected in Costa Rica as subspecies *P. m. costaricensis*, due to the smaller size of males, compared to the Guatemalan specimens. This classification persists until now, comprising into the subspecies *P. m. mocinno* the specimens of Mexico, Guatemala, El Salvador, Honduras and Nicaragua, and in the subspecies *P. m. costaricensis*, specimens of Costa Rica and Panama (Solórzano & Oyama, 2009).

According to genetic and morphometric analysis, there are strong differences between the two subspecies of *P. mocinno* (Solórzano & Oyama, 2009; Schulz & Eisermann, 2017). The morphological difference between the two subspecies are basically that *P. m. mocinno* subspecies is heavier, bigger and have longer and wider tail cover feathers (Solórzano & Oyama, 2009; Schulz & Eisermann, 2017), also *P. m. costaricensis* are less golden toned (Johnsgard, 2000). In adult females of *P. m. mocinno* the breast band appears more smoke gray than dull yellow-lime, the bill color seems darkish gray instead of black, the head has a golden buffy brown color with a slight crest instead of a smoky gray color and without crest as described for *P. m. costaricensis* (LaBastille et al, 1972). Morphological, and acoustic differences in vocalizations, probably respond to the separation of more than three million years of the subspecies.

Natural History

Reproductive behavior

Pharomachrus mocinno breeds at high elevations in the cloud forest and at moves to lower sites outside the breeding season. The altitudinal migrations might respond to changes in fructification of the tree species they eat (Wheelwright 1983). The average of its usual elevation range has been estimated between 1000 and 2850 m (Fagan & Komar 2016). In Guatemala it has been observed at elevations up to 3100 m in Sierra de los Cuchumatanes in the breeding period (LaBastille 1969) and as lowest as 1000 m (Land 1970) in other periods of the altitudinal migrations.

The species is probably monogamous. Studies of radio-tagged individuals have shown that males and females formed a single pair maintained during the following three breeding seasons, and probably during their whole life cycle (Solórzano & Oyama, 2009). Individuals has been observed in groups during the courtship phase, in pairs during nest building, and solitary during incubation periods or when feeding chicks (Skutch, 1944; Wheelwright, 1983). Both, male and female share nest-making activities, incubation, and care of the young. The normal clutch is two blue colored eggs. Parents take turns for

incubation, dividing the 24-hour day into two turns of duty each (LaBastille & Allen, 1969).

Pharomachrus mocinno is an exclusive secondary cavity nester (Johnsgard, 2000), individuals modify abandoned woodpecker nest sites in dead tree trunks. Finding suitable cavities is a crucial aspect for the successful nesting of the species (Siegfried et al, 2010). Resplendent Quetzal couples occupy the abandoned cavity and enlarge it (Wheelwright, 1983). Primary cavity-nesting species includes the Northern Flicker (*Colaptes auratus*), the Acorn Woodpecker (*M. formicivorus*), and others. Some species of trees that have been identified for the nests are *Brosimum costaricanum* and *Pinus pseudostrobus*. Based on artificial nest experiments, no differences were observed in wood types used (LaBastille & Allen, 1969), meaning that other factors could be more important in the nest selection by *P. mocinno*. Apparently the most important factors that make a nest suitable for both *P. mocinno* subspecies is the relative height compared to the tree height, with an average of 0.77. The snag heights used by *P. mocinno* varies greatly in both subspecies with a range of 1.9 to 10.8 m for *P. m. costaricensis*, and 5.8 to 29 m for *P. m. mocinno*, nevertheless, there is no difference in the relative heights of nest heights respect to the trunk. Another factor making a potential nest suitable for *P. mocinno* is the decay of the abandoned hole, it is only after sufficient decay that the site is abandoned by woodpeckers and becomes available for the Resplendent Quetzals (Siegfried et al, 2010). After a couple of *P. mocinno* identifies a potential nest, from an abandoned cavity, they carve it. A pair of individuals is capable of removing several centimeters in depth of decayed wood, either to enlarge a woodpecker hole or to fashion a new nest. The act of digging could be important in the reproductive cycle of *P. mocinno* (LaBastille & Allen, 1969). Then the nest are often used by Resplendent Quetzals for several years until the snag finally collapses (Siegfried et al, 2010; Kern, 1968).

Threats and limiting factors

Human activity is the main factor threatening habitats of *P. mocinno*. While there are populations inside protected areas, there are still sites located outside the reserves with a high level of degradation. Large areas of cloud forest are cut every year for firewood, charcoal, lumber and in past decades for roof shingles. Agricultural practices, as burning of understory to provide pasture, has fragmented mostly the low parts of the mountains. In past years (approximately before 1980), the milpa system (traditional maize crops) was one of the most problematic causes of forest loss (LaBastille & Allen, 1969). Nevertheless, elimination of virgin forest in order to plant coffee, tea, quinine and rubber is also an important cause of fragmentation, mostly below 1500 m.a.s.l. (LaBastille & Allen, 1969; Pope & Harbor, 2014). The changes in land, mostly in the lower parts of the

mountains, can truncate the altitudinal migrations of the species, following tree fructification, if they lack forest in good conditions in the lower parts (Powell & Bjork). Other important human activities that have been reported impacting the habitat of *P. mocinno* are felling of trees to obtain wild honey (LaBastille & Allen, 1969).

Other important limiting factor for populations of *P. mocinno*, are the availability of nest cavities. Some problems involved are: a) incidence of death and slowness of decay among trees that are soft enough for individuals to fashion their nests in b) susceptibility of dead nest-trees to the elements and to natural destruction (LaBastille & Allen, 1969), and c) the relative height of the hole (Siegfried et al, 2010). An average of one dead stub per each 1000 m², suitable for nesting holes has been reported in Atitlan volcano (LaBastille & Allen, 1969).

Apart from decimation of populations through habitat destruction, direct poaching and trapping of individuals is another important factor causing mortality. Sales of dried birds or feathers to tourists and museum collectors has been another problem, as well sale of living captive individuals. The tail-cover feathers of Resplendent Quetzal still has a strong importance as precious materials (Skutch, 1944; LaBastille & Allen, 1969; Solórzano & Oyama, 2009).

Predation of *P. mocinno* can occur from several species: among others, the Grey Squirrel (*Sciurus griseoflavus*), the Kinkajou (*Potus flavus*) and the Ornate Hawk-eagle (*Spizaetus ornatus*), in Guatemala (LaBastille & Allen, 1969); the Margay (*Felis weidii*) in Costa Rica (Wheelwright, 1983). The Green toucanets (*Aulacorhynchus prasinus*) are dominant over Resplendent Quetzal and sometimes displace them from their perch (Santana & Milligan, 1984), they are also important predators, that can feed on eggs and chicks of *P. mocinno* (Wheelwright, 1983).

Defense

The iridescent green of males and females of *P. mocinno* probably works as a protective camouflage particularly effective during rainy conditions (LaBastille et al. 1972). Shuttler and Weatherland (1990) suggested that in species with a strong predation pressure, sexual selection could be constrained, thus a little plumage dimorphism might be observed. This could explain why male individuals are only slightly more brilliant than females and suggests that their structural green is basically a cryptic adaptation (LaBastille et al. 1972). In wet or rainy conditions, the green bright color could be mistaken with the forest canopy. Nevertheless, in sunlight, the feathers reflect the light, being more brightly conspicuous than without sunlight conditions (LaBastille & Allen, 1969).

Feeding behavior and ecological role

The Resplendent Quetzal is an important seed disperser. As the other members of the family Trogonidae, *P. mocinno* adults are mainly frugivorous; however they feed their chicks also with insects and small vertebrates (Snow, 1981). Adults have a specialized behavior on feeding, probably in coevolution with the plant family Lauraceae, and it has also been suggested a relationship between the maturation of fruits of different species and the bird's altitudinal migrations (Wheelwright, 1983). The size of *P. mocinno* lead the bird to feed on relatively large fruits (*i.e.* 35 x 18 mm size of *Beilschmiedia* sp. and *Nectandra* sp.) and regurgitate seeds (Santana & Milligan, 1984).

Members of the Trogonidae family have weak legs, which hampers hopping and reaching for fruits from perch, as do other species feeding on the same fruits, like toucanets. Instead of feeding from perch, *P. mocinno* use the method of sallying (Santana & Milligan, 1984). Sallying is an aerial foraging mode consisting on catching insects or fruits in the air, but returning to a perch to feed (Avila et al, 1996). Before an individual sally, they scan their surrounding area for fruits, and then they usually take only one fruit per flight. Thus, the energy obtained from that unique fruit must compensate the costs of sallying for it. In order to meet this requirement, it is important for the individuals to recognize the quality of a fruit and be selective (avoiding small size, early stage of ripeness, low energy, low nutrient content or poor location) (Santana & Milligan, 1984). Individuals generally take ripe fruit, discarding the rotten ones (Avila et al, 1996). The amount of resources available for each species in an area, is linked to their food selection method, and also could be linked to other aspects of the species ecology. For example, Resplendent Quetzals are altitudinal migrators, while toucanets are not (Santana & Milligan, 1984). *Pharomachrus mocinno* individuals generally regurgitate the seeds in viable condition 15-30 min after ingestion. Generally *P. mocinno* individuals spent less than 2 min per foraging visit to fruiting trees (Wheelwright, 1991), so the seeds have a great possibility to be regurgitated in a place away from the feeding tree. The extreme specialization of *P. mocinno* to feed on some plant species, combined with the highly selective behavior, choosing only high quality fruits, makes of *P. mocinno* a key species on the regeneration of the cloud forest.

The chicks are mainly insectivorous, but also feed on small vertebrates. Adults feed the chicks during the first 10 days after hatching, including insects (mostly beetles, lepidopteran larvae, orthopterans and odonatans), small lizards and snails (Avila et al, 1996).

Cultural importance

The Resplendent Quetzal is the center of the past and present Mayan culture heritage. It is considered for many birders as one of the most beautiful birds on Earth, and maybe the first in splendor in the Neotropics (LaBastille & Allen, 1969; Skutch, 1944; Johnsgard, 2000). In addition to its beauty, the Resplendent Quetzal is also one of the most widely known bird in popular culture (Skutch, 1944).

In the Mayan culture, the Resplendent Quetzal represented the god Q'uk'umatz, or Feathered Serpent, one of the most important deities. For the Mayas, the Feathered Serpent created humanity together with the god Tepew (Falla, 2013). Q'uk'umatz is considered to be the equivalent of the Aztec god Quetzalcoatl, and the Mayan god Kukulcan of the Yucatan area (Declercq et al, 2004). In Figure 9 is shown a representation of Q'uk'umatz in the act of carrying Hunahpu, the avatar of the sun god Tohil. The Feathered Serpent, Quetzalcoatl, held a place in the pantheon of gods among Aztecs, Toltecs and Mayas.



Figure 9: Representation of Q'uk'umatz, the feathered serpent. Mixco Viejo, Guatemala (Picture: Coco García)

The feathers of *P. mocinno* were considered more precious than gold or jade by the Mayas (LaBastille & Allen, 1969). But also for Aztecs, however only a small proportion

of the area occupied by this culture falls within the known distribution of *P. mocinno*. The Aztecs demanded Resplendent Quetzal feathers for ceremonial purposes to other areas. The feathers were an important tribute item, they were appreciated for their symbolic value but also for their rarity. The estimated yearly tribute in Resplendent Quetzal feathers, only for the Aztecs, required the harvest of 6200 to 31,000 individuals. Probably the feathers were harvested without killing the individuals, nevertheless this could affect breeding activities, affecting populations (Peterson & Townsend, 1992).

In addition to feathers, other important products, were jade, obsidian, salt, cacao beans (as money) and copal trees (for incense and rubber) (Brewbaker, 1979). The feathers were used also in the elaboration of headdress for the emperors. One extreme example is the Montezuma's (1466-1520) headdress (Figure 10), an Aztec emperor. The headdress is considered one of the most important symbols of the pre-Hispanic history; the object is made with more than 400 quetzal tail-cover feathers. Nowadays the headdress is exhibited in the Ethnology Museum of Vienna. In 1940 a replica was made in Mexico and is now exhibited at the Museo Nacional de Antropología e Historia (Corona, 2014).

The importance of the Resplendent Quetzal for the Mayan cultures is evident. The species is represented in all kinds of arts and tools, in Figure 11 is shown an example of the representation in ancient objects. Furthermore, nowadays, the Resplendent Quetzal is also represented in the costumes, traditional dresses, handmade objects, and contemporary art (Figure 12).

A phenomenon happening at the Mayan city of Chichen Itza, evidence the highly advanced astronomic and mathematical knowledge of the civilization. In each spring equinox a “descending feathered serpent” can be seen in the temple of Kukulcan. A shadow appears on the north-west balustrade of the staircase of the temple, ending with the illumination of the head of the Feathered Serpent (Lubman, 2008) (Figure 13)

Furthermore, the representation of the Resplendent Quetzal was not only restricted to visual arts. In several Mayan temples of Tikal, Chichén Itzá, and other cities, an interesting acoustic phenomenon occurs. If somebody claps in front of some temples, an echo can be heard that resembles the vocalizations of *P. mocinno* (Figure 14). The phenomenon has been known for local guides and people since decades ago. The characteristic echoes are produced by a physical phenomenon, due to the shape of the stairs (Declercq et al, 2004), but is still uncertain whether the Mayan architects designed the temples in order to cause this particular echoes to resemble *P. mocinno* vocalizations, or if it was not a deliberate design. Nevertheless, being so important the Resplendent Quetzal for Mayan people, and considering the highly advanced mathematics they

developed, the fact that they constructed the temples thinking to produce these echoes is a very plausible hypothesis (Lubman, 2008; Declercq et al, 2004).



Figure 10: Moctezuma's headdress, with a height of 116 cm and a diameter of 175 cm, is considered one of the most important symbols of the pre-Hispanic history. The headdress is made with 400 tail-cover feathers of *P. mocinno*. It was a gift from the Aztec emperor Moctezuma to the Spanish conqueror Hernán Cortés at his arrival to America in the XVI century. In the present the headdress is exhibited in the Weltmuseum of Austria (Ethnological Museum of Vienna), and its ownership has been discussed between Mexico and Austria, causing tension in the relationship between the nations. Nevertheless, it has been not recommended the transportation of the object to Mexico, because it would damage the headdress, which is fragile (Corona, 2014) (Picture: weltmuseumwien.at / KHM with MVK and ÖTM)

Nowadays, the importance of the Resplendent Quetzal for the human populations of Mesoamerica still persists. The species was declared the national bird of Guatemala in 1871, and its day is celebrated on September 5 each year. Furthermore, in 1925 the Guatemalan Government declared the Quetzal as the national monetary unit (Banco de Guatemala, 2005) (Figure 15).



Figure 11: Representation of *P. mocinno* in an ancient ceramic container (Museo Popol Vuh) (Picture: Wikimedia)

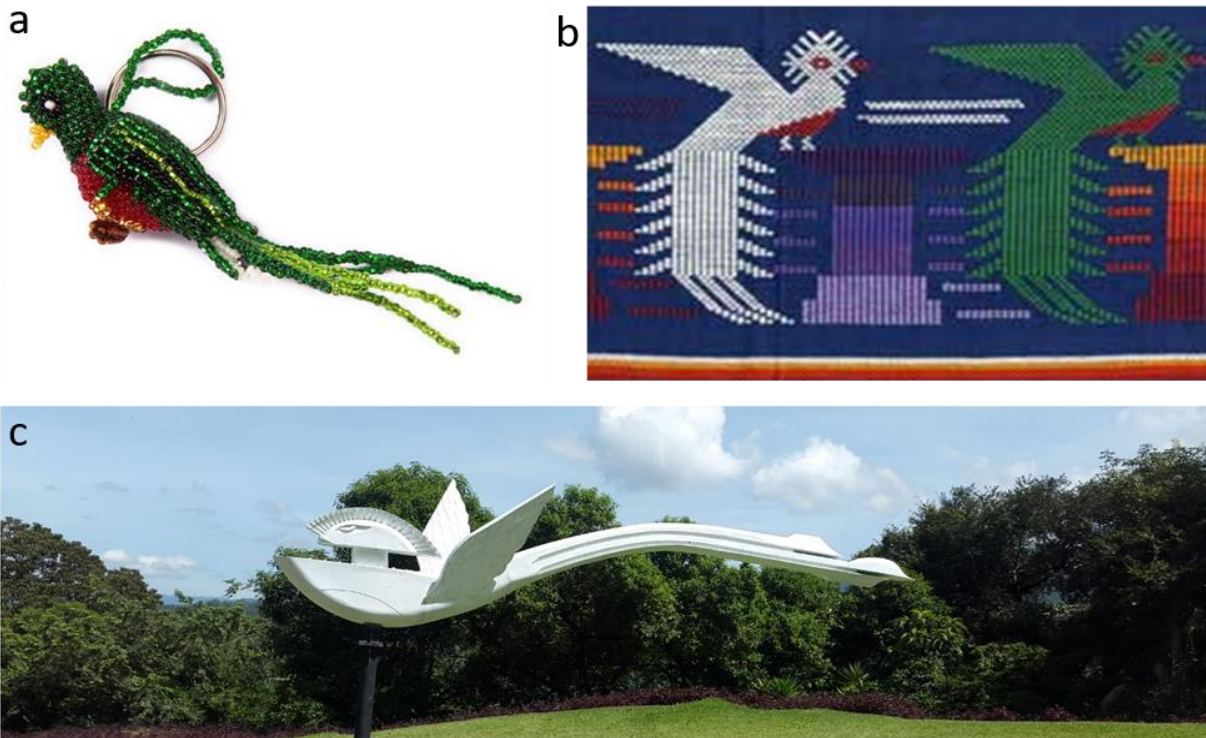


Figure 12: Artistic representation of *P. mocinno* in contemporaneous art. a) Keychain, b) Textiles, c) Sculpture by Efraín Recinos (Pictures: Pablo Bolaños, Wikimedia)



Figure 13: Feathered serpent “descending” phenomenon, for the autumn equinox in the temple of Kukulcan, Chichén Itza, Chiapas (Wikimedia)

The Resplendent Quetzal represents freedom in local traditions of Guatemala. There is a belief that the species dies in captivity. Nevertheless, it has been possible to maintain individuals and the reproduction in captivity of the species, in the zoo Miguel Álvarez del Toro-ZOOMAT in Tuxtla Gutiérrez, Chiapas (Morales-Divas, 2017). However, the captivity of the species remains a challenging task, which requires a high technical knowledge, not being possible without fulfilling various strict conditions. Thus the representation of freedom of the species still persists in the imaginary of the Guatemalan people. Also supporting the symbol of freedom of the Resplendent Quetzal, there is a legend in Guatemala that explains the red colour of the pectoral feathers of the species. The legend says that in a battle between the Mayan hero Tecún Umán (Figure 16a) and the Spanish conqueror Pedro de Alvarado, the first nailed his spear in the chest of Alvarado’s horse, then Tecún Umán was killed by the sword of Pedro de Alvarado. The legend says that a Resplendent Quetzal perched on the bleeding Tecún Umán’s chest, so the colour of the pectoral feathers of *P. mocinno* remained red (Palma-Ramos, 2002). This myth persisted until present times, supporting the symbol of freedom represented by the Resplendent Quetzal.

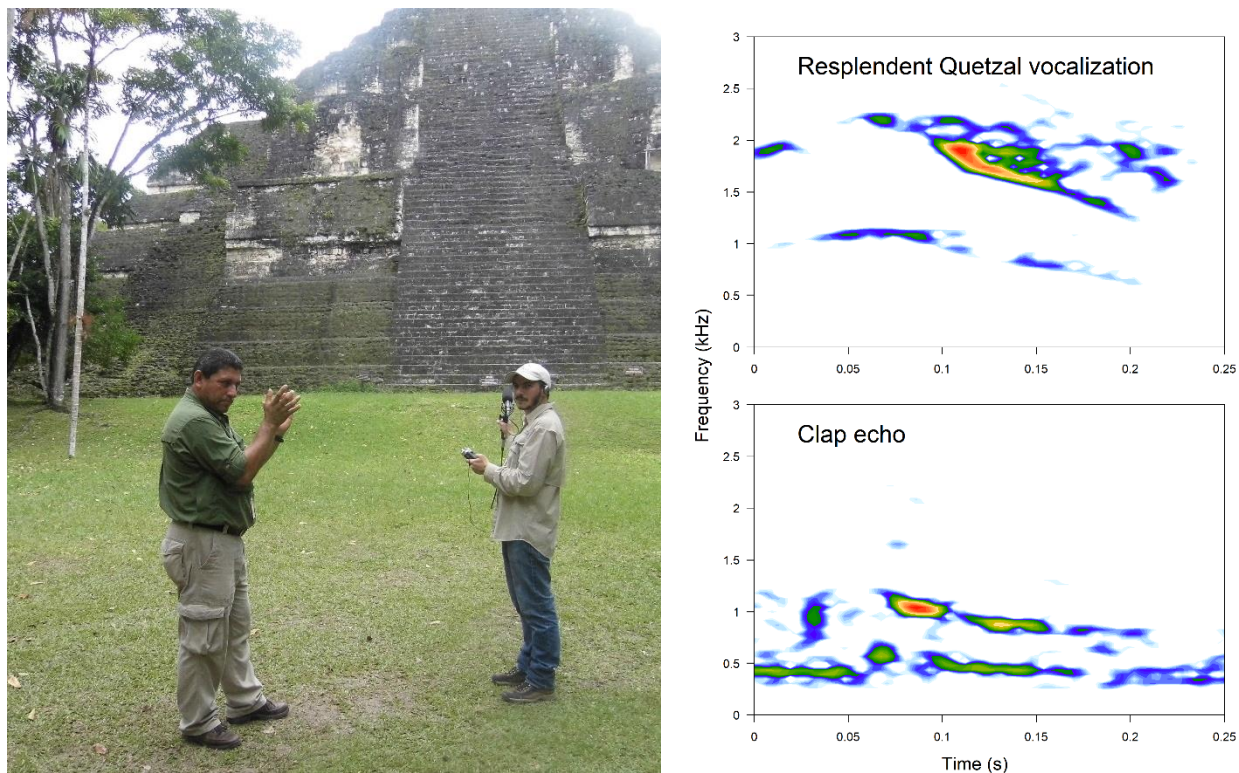


Figure 14: If someone claps in front of a Mayan temple like this in Tikal, it can be heard echoes resembling vocalizations of the Resplendent Quetzal. It is not clear if the Mayas designed the temples deliberately to produce this phenomenon, but the importance of the species for them makes this hypothesis possible (Picture: Pablo Bolaños 2014). Graphs at the right show a spectrogram of an alarm vocalization of *P. mocinno* and the sound of a clap echo, there are differences in frequency, nevertheless there are similitudes, for example both spectrograms have two harmonics, the upper harmonic being the most energetic

Perched above a parchment containing the legend “Libertad 15 de septiembre de 1821” (Freedom 15th September 1821), the Resplendent Quetzal figures in the flag shield of Guatemala. The date corresponds to the national independence day of Guatemala from Spain (Figure 16b). The figure of the bird appears also in many official buildings and gives name to the most important award in Guatemala the “Orden del Quetzal”. Evidencing and supporting the respect of the Guatemalan people towards the species, there is a national law established in 1875, which prohibits killing, trapping, or exporting the specimens of *P. mocinno*, dead or alive, or molesting their nests (LaBastille & Allen, 1969).



Figure 15: The Quetzal as monetary unit (Wikimedia). In the past, Mayan people utilized the tail cover feathers as monetary unit (picture: Wikimedia)



Figure 16: a) Statue of the Mayan hero Tecún Umán in Quetzaltenango, Guatemala. The hero has a headdress made of *P. mocinno* feathers. Legend says, that the red color of *P. mocinno* pectoral feathers arose when a Resplendent Quetzal perched on Tecún Umán, injured after a battle against the Spanish conqueror Pedro de Alvarado in Quiché department, Guatemala. b) The Resplendent Quetzal figures in the national flag shield of Guatemala, where it represents freedom. The bird is perched on a parchment with the inscription “Libertad 15 de septiembre de 1821” (Freedom September 15th 1821), the day of independence of Guatemala from Spain (picture: Wikimedia)



Figure 17: Refugio del Quetzal protected area in San Marcos department, Guatemala. The reserve is known as a place to practice birdwatching, specially the observation of *P. mocinno*

***Pharomachrus mocinno* as a flagship species**

Charismatic animal species, usually large vertebrates, have been used to attract interest and to focus conservation efforts. Organisms with these characteristics are known as flagship species. Flagship species can be used to lead a conservation campaign because it awakens public interest and sympathy (Simberloff, 1998). Most flagship species are large mammals, other groups as birds are uncommon. One exception is the Resplendent Quetzal, which has been widely used as flagship, being the symbol of natural reserves and conservation campaigns along its area of occurrence (Figure 17). Beside the attraction of conservation efforts, conservation areas having populations of the Resplendent Quetzal, benefit from the visitors who arrive with the intention to observe the species, being an important source of income helping to the continuation of the protection activities. At the same time, the protection of the Resplendent Quetzal helps to protect the cloud forest where it occurs, including other endangered species who depend on this habitat type.

The Resplendent Quetzal cohabits with other species, which also depend on the cloud forest to occur. The cloud forest is one of the most biodiverse habitat type of tropical areas, in addition, as other mountain forests of the zone, has a high degree of endemism. Some bird species endemic to mountain forests, comprising the cloud forest of the study area are, the Blue-throated Motmot (*Aspatha gularis*) and the Highland Guan (*Penelopina nigra*) among others. These species, together with *P. mocinno* interact between them, competing for ecological resources, as they are part of the same ecological community.

Ecological communities

Definition

An ecological community can be defined as an assemblage or collection of species found in a particular area or habitat. The species in a community interact between them. The interaction can be positive for one species and negative for the other, like in predation, parasitism or herbivory. The interaction can be negative for both species like in competition. The interaction could be one sided negative and null for the other, like in amensalism. The interaction could be positive for both species involved like in mutualism. And the interaction, could be positive for one species, but null for the other like in one sided commensalism (Morin, 2011). Ecological interactions between species could result from the use of common resources like food, nest sites, and even for acoustic space.

The Resplendent Quetzal is part of a peculiar community where it competes for ecological resources with other species. Competition for food occurs with species of birds like those of the family Ramphastidae (toucanets), Cotingidae (bellbirds) and Trogonidae (trogons and quetzals), among others. They are attracted to trees like those of the family Lauraceae, thus, they often feed together on the same species of fruits, which leads to a competition for this resource (Santana & Milligan, 1984). It has been observed that toucanets are dominant over Resplendent Quetzals, and sometimes displace them from their perch (Santana & Milligan, 1984).

If species use the same resources, the method to use the resource could be different among the different species avoiding overlap. For example, unlike toucanets that fed on the upper parts of the trees, *P. mocinno* fed mostly in the lower portions. So, a vertical segregation occurs between *P. mocinno* and *A. prasinus*, which might be associated with the tree's structure. The disposition pattern of fruits at the upper portion of the tree impose many obstacles to birds that feed using the sallying method, like *P. mocinno*, which needs open spaces. Another difference with toucanets is that the individuals of *P. mocinno* search for quality fruits before sallying for it, ensuring the effort compensation, implicit by the feeding method. In contrast, toucanets are less selective, trying to take as many of fruits they encounter, regardless their quality (Santana & Milligan, 1984). Those are examples of niche partitioning, that can be seen also by the use of other resources of each species, like the nest sites, or acoustic space.

The acoustic space can be defined as a multidimensional space with axes composed by acoustic features, such as dominant frequency, duration, number of notes, and other attributes that characterize the structure of a signal (Miller, 1982). Signals close together

in acoustic space, could have more potential to interfere between them if they occur at a specific period of time. For that reason, individuals may choose to sing in times and places that reduce acoustic interference. Thus, acoustic space can be studied as a resource subject to competence in an ecological community. The set of sounds of a defined community can be named as an acoustic community.

Acoustic communities

An acoustic community is a collection of sounds produced by all living organisms in a given habitat over a specified time (Gasc et al, 2013). Species in an acoustic community compete for the acoustic space. Vocal species sharing the same acoustic space would avoid or reduce acoustic overlap, therefore an acoustic niche hypothesis (Krause, 1993) predicts a frequency and/or a temporal partitioning (Farina et al, 2011).

Acoustic partitioning has been studied in anurans (Stanley et al, 2014; Chek et al, 2003; Duellman & Pyles, 1983; Luddecke et al, 2000; Martins, Itamar et al, 2006; Acevedo & Villanueva-rivera, 2006; Sinsch et al, 2012), birds (Stanley et al, 2016; Vokurková et al, 2018; Planqué & Slabbekoorn, 2008), crickets (Schmidt et al, 2013; Schmidt et al, 2016; Schmidt & Balakrishnan, 2014), interactions between birds and insects (Luther, 2009; Stanley et al, 2016), to mention some examples. Acoustic partitioning has been studied also in water environments, such as fresh water habitats (Gottesman et al, 2018) and marine environments, including fish and whales (Ruppé et al, 2015; Opzeeland & Boebel, 2018; Au et al, 2000).

Acoustic communities can occur in aquatic or terrestrial environments. Each acoustic community has its own characteristics, defining its own acoustic signature. According to the frequency, the communities could be classified as, infrasonic (<0.02kHz) including the whales (Cetaceae) or elephants (Elephantidae); ordinary, including the majority of vertebrates 0.02-20 kHz, like birds; or ultrasonic >20 kHz, including bats (Chiroptera), dolphins (Cetacea), shrews (Soricidae), some birds of the orders Caprimulgiformes and the family Apodidae, and some insects (Farina & James, 2016). Nevertheless, acoustic communities could be also classified and studied according to the habitat type, season or time of day, animal groups, and others.

The acoustic signature of each species can be used to measure the acoustic niche overlap and range of the entire community. The niche overlap measures the degree of potential competition between two or more species (Farina & James, 2016).

Emission of sound in a community is influenced basically by two factors. Bird songs are adapted to optimize their transmission distance in their usual habitats (Morton, 1975; Wiley & Richards, 1978). Acoustic adaptation hypothesis (AAH) first defined by

Morton (Morton, 1975) helps to explain variation in acoustic signal between populations differing in the environment structure of their habitats (Graham et al, 2017). Thus, the AAH leads to predict a convergence of the sounds produced by species sharing the same habitat and same time of singing. Hence, a convergence in songs is expected in birds living in the same habitat, for optimal transmission. But, on the other hand, species singing at the same time, should have a significant dispersion in the acoustic space, in order to avoid heterospecific interference (Luther, 2009). According to the acoustic niche hypothesis (ANH) (Krause, 1993), vocal species sharing the same acoustic space would avoid or reduce acoustic overlap, a concept deriving from the classic Hutchinson niche concept (Hutchinson, 1959). Thus, the ANH predicts frequency partitioning and/or temporal partitioning (Farina et al, 2011). In addition, both song features and singing behavior might evolve together (Luther, 2009).

Acoustic communities can be analyzed at different time scales. At a seasonal scale, change in the abundance of species of birds, derived from the arrival or departure of migratory species can be followed by the changes in the species structure, adding or reducing the complexity of the signature (Farina et al, 2013). The acoustic signature of anurans, also change along the different seasons (Martins, Itamar et al, 2006).

Acoustic communities also vary throughout the day, vocal activity of different species of birds, is different at dawn, dusk or night (Leopold & Eynon, 1961). Rodriguez et al. (2014) found a four period diurnal cycle in the acoustic community of birds in a tropical forest of the French Guiana. Acoustic space use of insects change also throughout the day and night, being so important that might drive the structure of the acoustic space use by other animal groups (Aide et al, 2017).

Changes in the acoustic signature can also be due to a change in the acoustic activity of different bird species. Preliminary studies on the communities of the cloud forest in Guatemala revealed that some species of birds tend to vocalize more actively in the first minutes of light incidence at dawn, then some minutes later these species decrease the acoustic activity and other species begin to vocalize (*personal observations*). In other animal groups, the acoustic activity peaks could be different, for example, Mediterranean male cicadas produce sounds when ambient temperature is at its maximum (Sueur & Sanborn, 2003). In aquatic animals, acoustic activity peaks can occur at night, like in the humpback whale (*Megaptera novaeangliae*) close to Hawaii Islands (Au et al, 2000), and in fishes in western Australia (Parsons et al, 2013). In ponds, it has been observed different peaks of activity according to the habitat characteristics of different ponds (Desjonqueres et al, 2015).

Changes in acoustic signatures are linked to changes in environmental features, such as vegetation cover, land mosaic structure, temperature, humidity and pH (for aquatic medium), as they can affect animal sound emission (Krause & Farina, 2016). In a rainforest in Costa Rica, Pekin et al. (2012) found a non-random pattern in the canopy structural attributes, identifying forest patches of high acoustic diversity, linked to the understory cover density and the presence of space in the canopy. Changes in species composition derive in changes of the acoustic signature, climate change is influencing species range expansion and contraction, for example, invasions of premontane species have been observed in a cloud forest of Costa Rica, providing evidence that climate change influences species distribution (Pounds et al, 1999a), These invasions can be tracked studying the acoustic community, making possible at the same time, to study the effects of climate change.

Being one of the most biodiverse ecosystems in the Neotropics the cloud forest provides uncountable opportunities to study acoustic communities. One important species part of the cloud forest community is the Resplendent Quetzal. The species imposes some behavioral and ethical issues to be taken into account. Therefore it is necessary to analyze the available alternatives, or to develop new methodologies to study individuals and track their populations.

Potential methods to study *P. mocinno* in its habitat

The greater challenge to make precise observations of *P. mocinno* is the height and density of the forest canopy in which individuals maintain their activities. Individuals dwell high in the canopy almost all the time, excepting throughout the nesting season, when they move and vocalize at lower heights when looking for nest-sites, or vocalize directly from the nests. Additionally, their plumage, colors and their perching behavior, staying static for long periods, make observations complicated (LaBastille & Allen, 1969).

Traditional methods

In order to study the species there has been used direct observation methods like line or point transects. Both methods are based on sightings of birds along a trail within a predefined survey unit. Line or point transects are the most used methods in many situations. These methods are efficient in terms of the quantity of data collected per unit of effort expended.

These methods have been used to examine bird-habitat relationships, deriving relative and absolute measures of bird abundance (Gregory et al, 2004). Transects can be

usefully supplemented, in combination with other count methods such as sound recording, mist netting and tape playback (Whitman et al, 1997).

Ecology and feeding behaviour of the Resplendent Quetzal has been studied by direct observation (Wheelwright, 1983; LaBastille et al, 1972; LaBastille & Allen, 1969; Skutch, 1944). Observation line transects have been applied with success to estimate abundance of Resplendent Quetzal in relation to fruit availability in a cloud forest of south-eastern Mexico (Solórzano et al, 2000); in addition, point count transects have been used to study the fruit phenology of the nutritious species that the Resplendent Quetzal includes in its diet in Guatemala (Bustamante et al, 2010); in both studies, a relation between the abundance of Resplendent Quetzals related to the abundance of the food species, has been found. Other methods like capture techniques, are often used when bird species are rarely seen or heard. In these cases, capture with mist nests could be a solution (Gregory et al, 2004). Capture techniques have been used widely in the tropics, combined with other methods (Whitman et al, 1997).

Tape playback is another method used specially with some species of birds, particularly difficult to see or hear (Gregory et al, 2004). Playback can be used also to tackle some taxonomic problems with species, looking for a response or discrimination of conspecific song (Freeman & Montgomery, 2017). Some attempts of playback experiments have been conducted with the Resplendent Quetzal (Solórzano & Oyama, 2009), nevertheless, to our knowledge, any formal playback experiment have never been done.

Birds can be tracked by radio telemetry or GPS devices. This requires the capture of individuals to install devices to track their movements in actual time. In Guatemala, Paiz (1996) found that individuals of Sierra de las Minas, can move from their breeding sites at 2,500 m.a.s.l. to sites as low as 1,200 m.a.s.l., displacing about 25 to 50 km. Telemetry, has also provided evidence for the lack of connection between the populations of *P. m. costaricensis* from Costa Rica, and the closest populations of *P. m. mocinno* of Nicaragua (Powell & Bjork, 1995). Telemetry has also been used with success in another study in Guatemala (Yurrita, 2013), finding that availability of well-preserved forest areas is necessary for the altitudinal migrations.

All the methods to study bird behavior or track populations show advantages but could also bear some issues. For example, in direct observations, human presence could affect behavior of the species. Differences may exist in the ability and experience to record and recognize bird species, and other data, between observers resulting in a potential source of bias. Capture methods can be time consuming and require substantial training to develop the skills needed to catch, and handle birds. In addition, to ensure the

safety and welfare of birds, methods requiring the use of mist nets are regulated and require a license in many countries. Despite mist netting can give important information on demographic parameters, such as survival and breeding success, some authors consider it a relatively poor method for surveying birds. With tape playback methods, is necessary to take care in order to reduce disturbance to a minimum, in addition due to the possibility to affect population size estimations, interpretations should be taken with precaution (Gregory et al, 2004). Radio and GPS tracking requires to capture individuals, and the quantity of individuals tracked might be low. Usually GPS and radio devices are expensive, capture of individuals could be time consuming, and it has the same ethical problems involved when trapping is required. In addition, the device itself could affect the activities of the individual surveyed, probably increasing its vulnerability to predation, or interfering with their normal activities (Mech & Barber, 2002).

Acoustic methods

An alternative method to study birds in their habitats consists in the recording and analysis of their vocalizations (Figure 18). The study of various bird species using acoustics have been applied with success. It has also been suggested that acoustic identification in recordings is a suitable alternative to point counts, for estimating species richness, and a more recommended method in some conditions (Haselmayer & Quinn, 2000). In addition, sound recording provides an effective method to track birds, it can eliminate or reduce biases due to observer differences in identification, the recordings can be archived, and it can solve issues due to unavailability of experts (Celis-Murillo et al, 2009). Acoustic methods could be effective to study species difficult to observe, but relatively easy to hear, like tropical or nocturnal birds. Acoustics have been used in studies of nocturnal birds like Scops Owls (*Otus scops*) (Denac & Trilar, 2006) and Great Horned Owls (*Bubo virginianus*) (Odom et al, 2013).

Acoustic analysis has allowed to determine bird territories. This has been applied for example, studying parrot flocks, which can be detected by their flight calls (Baptista & Martínez Gómez, 2002).

In addition, acoustic analysis has been more effective than morphology to determine the sex of birds. For example, it has been applied to study the Yelkouan Shearwater *Puffinus yelkouan*, due to a difference in the fundamental frequency of his call, between male and females on the 100% of the cases (Bourgeois et al, 2007). Differentiation of sex with acoustic analysis can be very useful for species without a strong sexual dimorphism, like the Horned Guan (*Oreophasis derbianus*). The knowledge about sex proportion on bird populations is an important component on ecological or

conservation projects. The determination of sex proportion by bioacoustics has been conducted also on the Socorro Mockingbird (*Mimodes graysoni*) (Baptista & Martínez Gómez, 2002). The use of acoustic analysis have been also useful to evaluate the pairing state of various species, solitary males being generally more actively vocal than the paired ones.



Figure 18: Recording of bird vocalizations using a Sennheiser ME-67 microphone connected to a Tascam digital recorder DR-100 MK II (picture: Pablo Bolaños)

Furthermore, by the analysis of bird calls, it has been possible to determine the identity of the emitters (Gregory et al, 2004). Individuality in voice have been demonstrated in various species, like in the Corncrake (*Crex crex*), which led to monitor the individuals, and to quantify the number of the population in an area (Peake & McGregor, 2001). Individuality has been also demonstrated in see birds (Charrier et al, 2001), and other species. In population size estimations, is possible to apply capture-mark-recapture methods to re-sightings based on vocalizations (Gregory et al, 2004).

The use of recordings to study the Resplendent Quetzal has been recommended a few decades ago (LaBastille & Allen, 1969), nevertheless until now, their vocalizations were not quantitatively described, and there was no research on the species based on acoustic methods. The use of recording devices, is completely non-invasive, thus being in concordance with local traditions.

Acoustic methods could have some bias regarding the experience of the identifier of the target species in a survey. Nevertheless, with automatic detection methods, the error rates can be determined, which in human based detection methods can be difficult or not possible to quantify (Katz et al, 2016a). Furthermore, automated detection methods are robust and highly accurate, offering a suitable and efficient alternative to field observer point counts monitoring (Digby et al, 2013). In addition, due to the large quantity of recordings obtained with the availability of automatic detection units (ARUs) (Figure 19), Automatization of detection provides a faster way for the species identification.

Automatization of acoustic methods

In the last decades, ARUs have made possible to record several hours of sounds, simultaneously at different sites (Acevedo & Villanueva-rivera, 2006). ARUs can be deployed in remote and highly inaccessible sites and can be programed to record vocal activity over specified times and periods. The high quantity of data generated became challenging and time consuming to analyse manually, thus automated detection methods have attracted the attention of scientists, and are increasingly used for species identification and monitoring of large scale studies (Katz et al, 2016b).

Automatic detection systems have been applied with success in studies on various groups of animals, like elephants (Keen et al, 2017), insects (Jeliazkov et al, 2016), birds (Goh, 2011; Oliver et al, 2018; Goyette et al, 2011; Agranat, 2007a), and others. Many automatic detection methods based on algorithms have been employed to study birds, with positive results (Priyadarshani et al, 2018; Agranat, 2007b; Knight et al, 2017b). In bird monitoring programs, it has been recommended the complementation of point count methods, with automated acoustic detection, having both methods strengths and weaknesses (Leach et al, 2016). In addition, it has been suggested that, with a proper sampling protocol, automated acoustic detection methods offer a highly efficient alternative to human observer point counts (Digby et al, 2013). With single species surveys, it has been found that automated identification methods are effective in determining the presence of the Common Nighthawk (Knight et al, 2017b).

In automated detection methods, it is possible to calculate errors in identification. The results of automatic identification can be manually validated by the researcher to identify true positives from false positives (Knight et al, 2017b). In a monitoring program based solely on human observers, it could be difficult to quantify errors in identification caused by different identifiers with unequal experience or preparation. The automated species detection methods require to train a computer to detect, identify and classify an acoustic event, belonging to a target species vocalization (Knight et al, 2017b). All the

methods of automatic detection, compare sounds in a survey to a template (Katz et al, 2016b), then evaluates the fit of the acoustic signal in the recording (Knight et al, 2017b), assigning a score. According to the objectives of the study, the researcher selects a score threshold, above which a detection is classified as a true identification (Katz et al, 2016a). If the chosen score threshold is high, true positive identifications increase, but also the false negatives. Similarly, if the score threshold is low, the false negative identifications decrease, but also the true positives. Then, the score threshold chosen depends on the objectives of a study.



Figure 19: Autonomous recorder Wildlife Acoustics® SMII in Los Andes protected area, Guatemala (picture: Pablo Bolaños)

Automated acoustic monitoring could solve issues regarding the costs and availability of experts in the field, in addition, automatic detection can be used to analyze large datasets, faster and with a known error rate. In addition, eliminating human presence in the habitat surveyed may decrease or eliminate the bias caused by changes in behavior of the species surveyed. These characteristics could be substantial in monitoring programs or behavioral studies of species difficult to observe, or not suitable to study by other methods, due to ethical issues, or with a high cultural relevance.

Aims and outline

Gaps in our knowledge

The velocity of habitat destruction is faster than the scientific capacity to document and study the species and the populations (Krause, 1999). Recording of tropical birds is an important tool for their study and conservation. The studies and basic descriptions of bird

vocalizations, can be useful as a base for posterior researches and for management purposes.

The cloud forest is one of the most threatened habitat types in tropical areas. Its unique characteristics, makes them vulnerable to habitat fragmentation and climate change (Pope & Harbor, 2014; Still et al, 1999). Although it is not the most biodiverse tropical habitat, the level of endemism found in resident animal species is exceptional. For example, 32% of Peruvian endemic vertebrates are localized in cloud forests. The conservation status of these unique ecosystems is precarious as they are among the most endangered of all tropical forest types (Still et al, 1999).

Pharomachrus mocinno is one of the species restricted to the cloud forest. Despite the high cultural and ecological importance of *P. mocinno*, and the species has a high priority for research, the status of the populations is unknown, but it seems to be decreasing (Birdlife International, 2016). The absence of an effective non-invasive method to study the species, could be the reason of this lack of knowledge.

In addition, it has been suggested that the two subspecies of *P. mocinno* recognized until now, are two different species. The separation in two species would decrease the area of occurrence, which would have strong consequences for its conservation status.

It is urgent to have a reliable non-invasive method to study the Resplendent Quetzal. An automatic detection method would be ideal for the purposes, considering the behavioral characteristics of the species and its cultural importance. One necessary step for the system development, is to first describe the vocalizations, then it would be the base to support a species differentiation hypothesis important to clarify its conservation status, also the base to develop models for the automatic detection system, and finally, an analysis of acoustic bird community in its habitat would help to identify the species overlapping with the vocalizations of *P. mocinno*, which will help to reduce the error rates of the automatic detection system.

General Problematics

The general aim of this thesis is to investigate the acoustic behavior and ecology of the Resplendent Quetzal, *Pharomachrus mocinno*, in the cloud forest of Guatemala.

Outline

Chapter 1

What is the vocal repertoire of *P. mocinno*? What are the main acoustic properties of the vocalizations? How do these vocalizations propagate through the cloud forest? Knowledge of the behavior of the species exists, but its vocalizations have never been

described. A full description of the vocalizations of *P. m. mocinno* according to the behavioral context was made. In order to describe better the function and acoustic properties of each vocalization, sound propagation experiments were included. This helped to quantify the distance that each vocalization type can travel in the habitat, so, short and long range calls could be identified, and the possible function of communication was explained. Classification of the different calls helped to choose the most appropriate call type to use in an acoustic monitoring system.

Chapter 2

Are the subspecies *P. m. mocinno* and *P. m. costaricensis* different species? Do their vocalizations significantly differ?

Based on morphometric and genetic studies, it has been suggested that *P. mocinno* must be separated into two species. Nevertheless, behavioral difference has not been quantified. Difference in vocalizations has been useful to clarify taxonomic status of different species. In order to respond a species differentiation hypothesis, a quantification of the difference in the territorial vocalizations of the subspecies was held by multivariate analysis. The results showed a clear differentiation in their vocalizations, supporting the erection of the subspecies into different species.

Chapter 3

It is possible to track the presence of *P. mocinno* in the field with automatic recordings? What are the space and time dynamics of an acoustic population of *P. moccino*?

Automatic recording units were installed over two consecutive years in a cloud forest of Guatemala. Then an automated acoustic recognizer was developed, based on cross correlation method. Results were analyzed to determine if weather conditions could influence the acoustic activity.

Chapter 4

Does *P. mocinno* compete acoustically with other bird species belonging to the same acoustic community? To address these questions, all the species found in the bandwidth occupied by *P. mocinno* vocalizations were identified, then the potential overlap of the vocalizations of these species with *P. mocinno* was calculated, and the actual overlap was quantified. A multifactorial analysis was conducted including the overlapping difference (observed and potential overlap), and other ecological factors of competition.

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Chapter 1: Vocal repertoire of *Pharomachrus mocinno*



Cloud forest in the south slope of volcano Atitlán (picture: Pablo Bolaños)

1.1 Summary

1.1.1 Context

The Resplendent Quetzal *Pharomachrus mocinno* is considered in a high risk of danger in Guatemala and its commerce is regulated internationally. The species is included in the IUCN red list of threatened species. Anthropogenic activities have a negative impact on the quality of its habitat, inducing a severe decline of populations. The Resplendent Quetzal is important as a seed disperser and is the centre of the past and present Mayan culture.

1.1.2 Problematics

The available studies about the species have covered aspects of the natural history and biology. Nevertheless, there is no description of the acoustic repertoire, which is necessary to better understand the behaviour of the species.

1.1.3 Methods

In order to describe the acoustic repertoire, we recorded and collected in sound archives vocalizations of twelve individuals from six different localities distributed in Mexico and Guatemala. Propagation experiments of the vocalizations in its habitat were conducted to increase the knowledge about the function of the vocalization types categorized by our analysis.

1.1.4 Main results

We described for the first time four vocalization types of *P. m. mocinno*, among them, two are intended for long range, and two for short range communication.

1.1.5 Perspectives

The present study is fundamental to understand the communication system of the species. The results can be used to design acoustic monitoring protocols according to the objectives of the study and the characteristics of the sounds.

1.1.6 Related communications and publications

Vocalizations of a flagship bird species (*Pharomachrus mocinno*): implications for conservation status”. Bolaños, P., Aubin, T., Sueur, J. 2017. Oral presentation at the

annual conference of the “Société Française pour l’Etude du Comportement Animal”, Ile de France.

1.2 Introduction

The Resplendent Quetzal is a flagship species (Renner, 2003), with a high cultural importance along its distribution, being the most important national symbol in Guatemala. In addition to its social influence, the Resplendent Quetzal plays a significant ecological role by dispersing the seeds of at least 32 tree species and by participating to the dynamics and resilience of the cloud forest (Solórzano et al., 2000). The species completes altitudinal migrations related to the availability of the fructification of the tree species they feed on (Powell & Bjork, 1995). It has been suggested that there could be a coevolution between the plant family Lauraceae and the Resplendent Quetzal (Wheelwright, 1983), being a key species for the dispersion of this plant family. *Pharomachrus mocinno* is ranked in the Near Threatened category of the IUCN Red List (Birdlife International, 2016) and listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora Appendix I of the most endangered species (UNEP-WCMC (Comps.), 2014).

Birds vocalize to communicate with other members of the same species. The communication could have conflict or cooperation purposes (Catchpole & Slater, 2008). Depending on the purpose of the communication, vocalizations could be relatively quiet or inconspicuous, if it benefits the receiver and sender; or could be louder if it have alarm or territorial purposes (Krebs & Dawkins, 1984).

Among the different species of birds, the capacity to learn vocalizations and the complexity of the signals they emit, is highly variable. Apart from the oscines in the order Passeriformes, hummingbirds (Trochilidae) and parrots (Psittacidae), there is no evidence that other species of birds could learn their vocalizations (Brown et al, 2006). Members of the family Trogonidae produce vocalizations that tend to be loud, repetitive and acoustically simple in both sexes. Male “songs” typically consist of multiple repetitions of the same note at fairly regular intervals, these signals are species and sex-specific, and have temporal association with pair formation or breeding. Other trogon vocalizations, are associated with disturbances, these sounds are chattering or chirring sounds (Johnsgard, 2000). Members of the genus *Pharomachrus* are relatively large and heavy, compared to other members of the same family. According to Johnsgard (2000), in larger species of the family Trogonidae, vocalizations are generally lower in pitch and louder.

Vocalizations of *P. mocinno* are undescribed, except for some onomatopoeic descriptions of the repertoire with functions as territorial advertising, recognition or

contact, courtship and alarm (LaBastille et al, 1972; Skutch, 1944; LaBastille & Allen, 1969).

Vocal descriptions provide a valuable instrument for population census surveys and monitoring, particularly for birds of conservation concern. It is important to promote both documentation and conservation actions to preserve *P. mocinno*, and a formal description of the vocalizations of this species is an important step.

Here are presented for the first time, the vocalizations and singing behaviour of *P. mocinno*. The present study is fundamental to understand the communication systems of the species. Recordings were collected during January and February 2016-2017 in Guatemala. An estimation of the active acoustic range of the repertoire was obtained with propagation experiments in the cloud forest. Our observations, analyses and propagation experiments show that the acoustic repertoire of *P. mocinno* is made of short and long range signals probably used for private and public communication respectively.

1.3 Material and methods

1.3.1 Vocalization repertoire

Vocalizations of *P. m. mocinno* were obtained through personal recordings recorded in Guatemala and recordings available in public archives. First, vocalizations of *P. m. mocinno* were recorded in January and February 2016 and 2017 during the peak of vocal activity in two protected areas of Guatemala: (1) the “Refugio del Quetzal”, San Marcos (N 14° 56' - W 91° 52', 1531 m) (Figure 20a), and (2) “Los Andes”, Suchitepéquez (14° 32' - 91° 11', 1992 m) (Figure 20b). The “Refugio del Quetzal” is a reserve including a 50 ha area at an elevation of 1800 – 2000 m, with a cloud forest fragment surrounded by cattle grazing. “Los Andes” is a private reserve including 607 ha on the southern slope of the Atitlán volcano at an elevation of 840 – 1830 m, with a cloud forest on the higher part of the reserve (364 ha) and crops of coffee, tea and rubber on the lower part (243 ha). In both areas, singing individuals were visually localized and recorded (Figure 21) using a Tascam digital recorder DR-100 MK II (44.1 kHz sampling frequency, 16 bit dynamic) connected to a Sennheiser ME-67 directional microphone (frequency response: 40-20000 Hz \pm 2.5 dB). Recordings made in “Ranchitos del Quetzal” protected area, in June 2013 and January 2017 were also included. “Ranchitos del Quetzal” is a private reserve that constitutes a continuation of the forest of the “Biotopo Mario Dary Rivera para la Conservación del Quetzal” protected area, which covers 5241 ha, which includes 1017 ha of cloud forest, with an elevation between 1670 and 2348 m (Yurrita, 2013). Second, recordings available in two sound libraries (Macaulay Library and Biblioteca de Sonidos

de Aves de México) were collected (Table 1). All sounds included were uncompressed wav files with a minimum sampling rate of 44.1 kHz and a dynamic resolution of 16 bit. The locations of all the recordings included are presented in Figure 22.

Table 1: Recording sites of vocalizations of *P. m. mocinno* used to describe the repertoire

Site	Country	Latitude	Longitude	Recordist
Sierra de las Minas	Guatemala	15.155538	-89.642746	A. Martínez
El Triunfo, Chiapas	México	15.666759	-92.800035	F. González
Reserva los Tarrales, Suchitepequez	Guatemala	14.56	-91.168	M. Medler
Los Andes, Suchitepéquez	Guatemala	14.54878	-91.183371	P. Bolaños
Refugio del Quetzal, San Marcos	Guatemala	14.942850	-91.871367	P. Bolaños
North of Emiliano Zapata, Chiapas	México	17.1666667	-92.4166667	F. González
El Triunfo, Chiapas	México	15.65	-92.8166667	F. González
Ranchitos del Quetzal, Baja Verapaz	Guatemala	15.215489	-90.219249	P. Bolaños
Refugio del Quetzal, San Marcos	Guatemala	14.940633	-91.872533	P. Bolaños
Los Andes, Suchitepéquez	Guatemala	14.546267	-91.1853	P. Bolaños
Los Andes, Suchitepéquez	Guatemala	14.546267	-91.1853	P. Bolaños
Ranchitos del Quetzal, Baja Verapaz	Guatemala	15.215489	-90.219249	P. Bolaños



Los Andes Reserve



Refugio del Quetzal Reserve

Figure 20: Cloud forest at the recording sites, Los Andes and Refugio del Quetzal Protected areas

The vocalizations were analysed with Raven Pro 1.4 software (www.birds.cornell.edu/raven) by measuring the following time parameters on the oscilogram (time precision = 0.0232 s) and frequency parameters on the spectrogram (frequency precision = 21.5 Hz): note duration (s), inter-note duration (s), inter-syllable duration (s), median frequency (Hz), highest and lowest frequencies (Hz), first and third frequency quartiles (Hz) (the frequencies that divide the selection into frequency intervals containing respectively 25% and 75% of the energy), inter-quartile-range (difference between the first and third frequency quartiles), and peak frequency (Hz). The number of

individuals taken in account for each vocalization type is given in Table 2. The figures of spectrograms were realized with the R version 3.2.5 (Development Core Team, 2008) package seewave version 2.0.5 (Sueur et al, 2008) with a Fourier transform made of 2048 samples tapered with a Hanning window and with an overlap of 87.5%.

1.3.2 Propagation of the vocalizations through the cloud forest

Propagation experiments were carried out at “Los Andes” to quantify the modification of the territorial, alarm, courtship and contact vocalizations emitted by *P. m. mocinno* at different distances.



Figure 21: *P. m. mocinno* in Refugio del Quetzal reserve (picture: Pablo Bolaños)

Sounds were synthesized on the basis of representative natural vocalizations previously recorded. Synthesized vocalizations were built using the graphic synthesizer of the Avisoft SASLabPro software version 4.15 (Avisoft Bioacoustics, R. Specht–version 3.74) that extracts the frequency contour of the fundamental frequency, the relative amplitude of the different harmonics and the amplitude envelope of the natural vocalization. This procedure ensured to use sounds that do not contain any background

noise. One synthetic sound was built for each of the four vocalization types, and edited in a single sound file with 15 repetitions of each vocalization (Figure 23).

The series of synthetic sounds was played back with a loudspeaker FoxPro Fury 2 with sound pressure levels corresponding to the estimated natural levels of the calls emitted by the species (80 dB_{SPL} for the territorial call, 82 dB_{SPL} for the alarm call, 69 dB_{SPL} for the courtship call and 56 dB_{SPL} for the contact call, all measured at a distance of 1m from the loudspeaker). The propagated sounds were recorded at a sampling frequency of 44.1 kHz and a 16 bit dynamic with a Sennheiser ME-62 K6 microphone connected to a Marantz PMD 661 recorder.

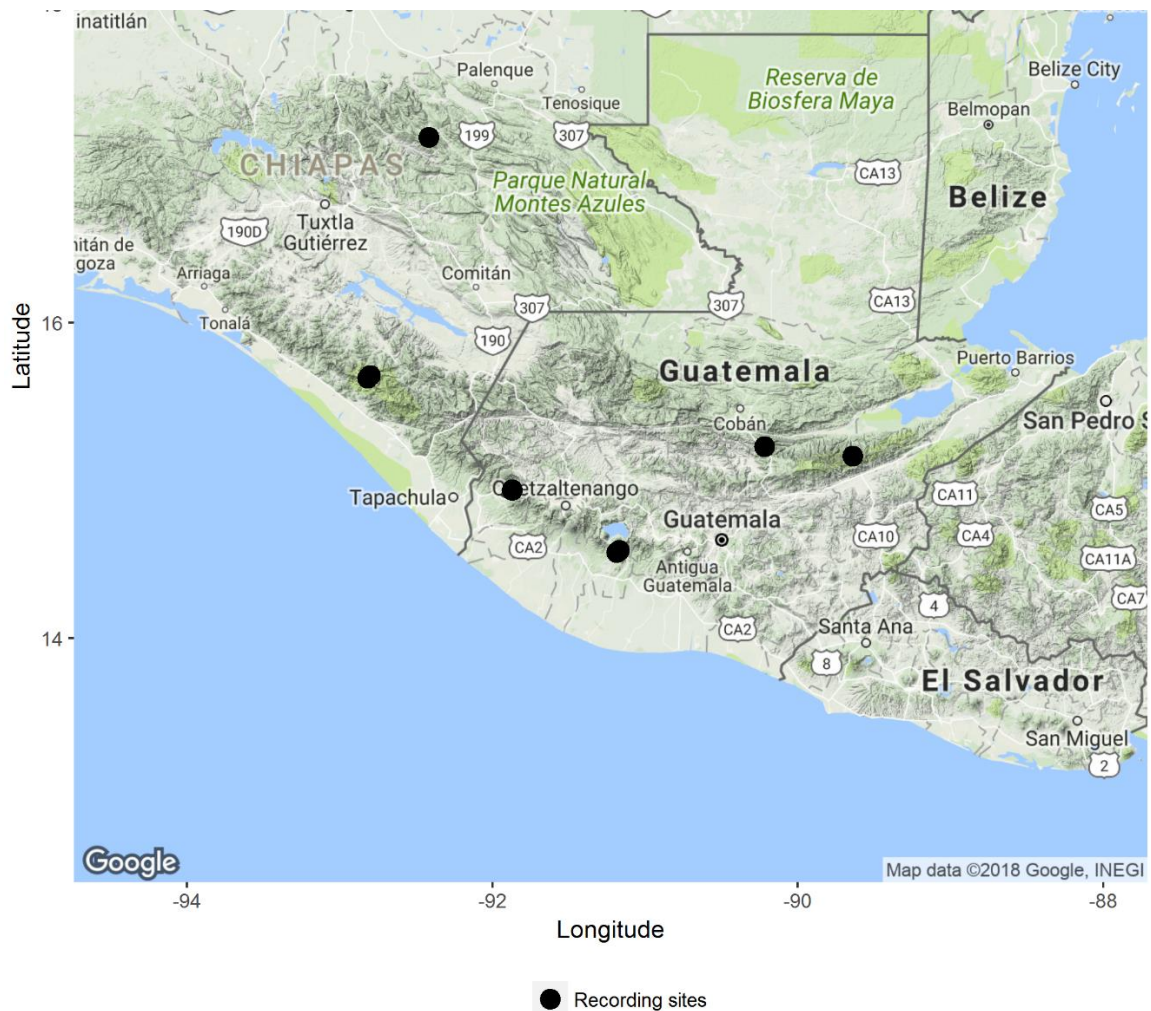


Figure 22: Map of the sites of recordings of *P. m. mocinno* (Google® background)

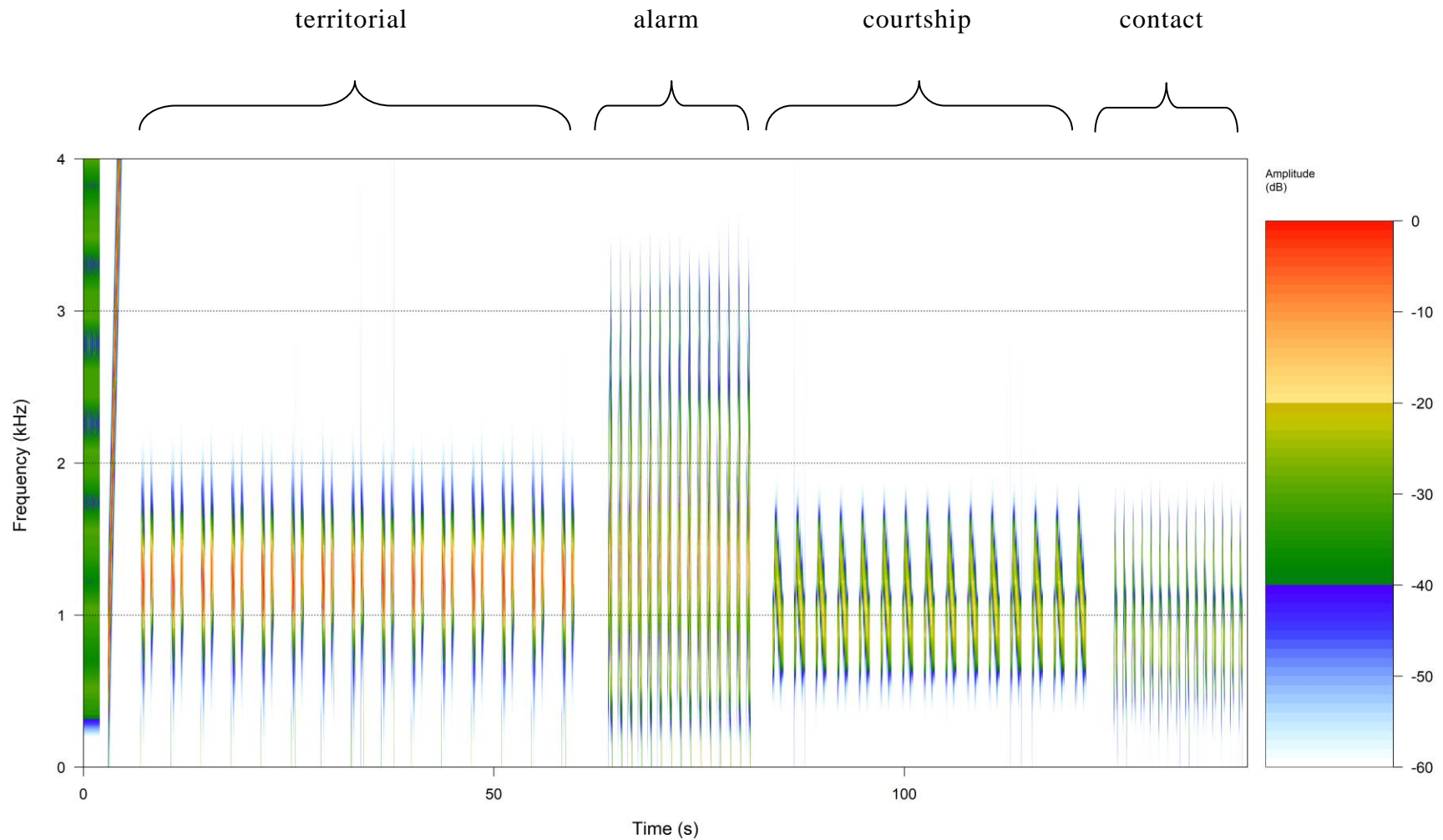


Figure 23: Synthetic signal of four vocalization types of *P. m. mocinno*, propagated through the cloud forest. The first sound, before the territorial vocalization, has guiding purposes in order to ensure the correct timing of the recordings in the analysis process

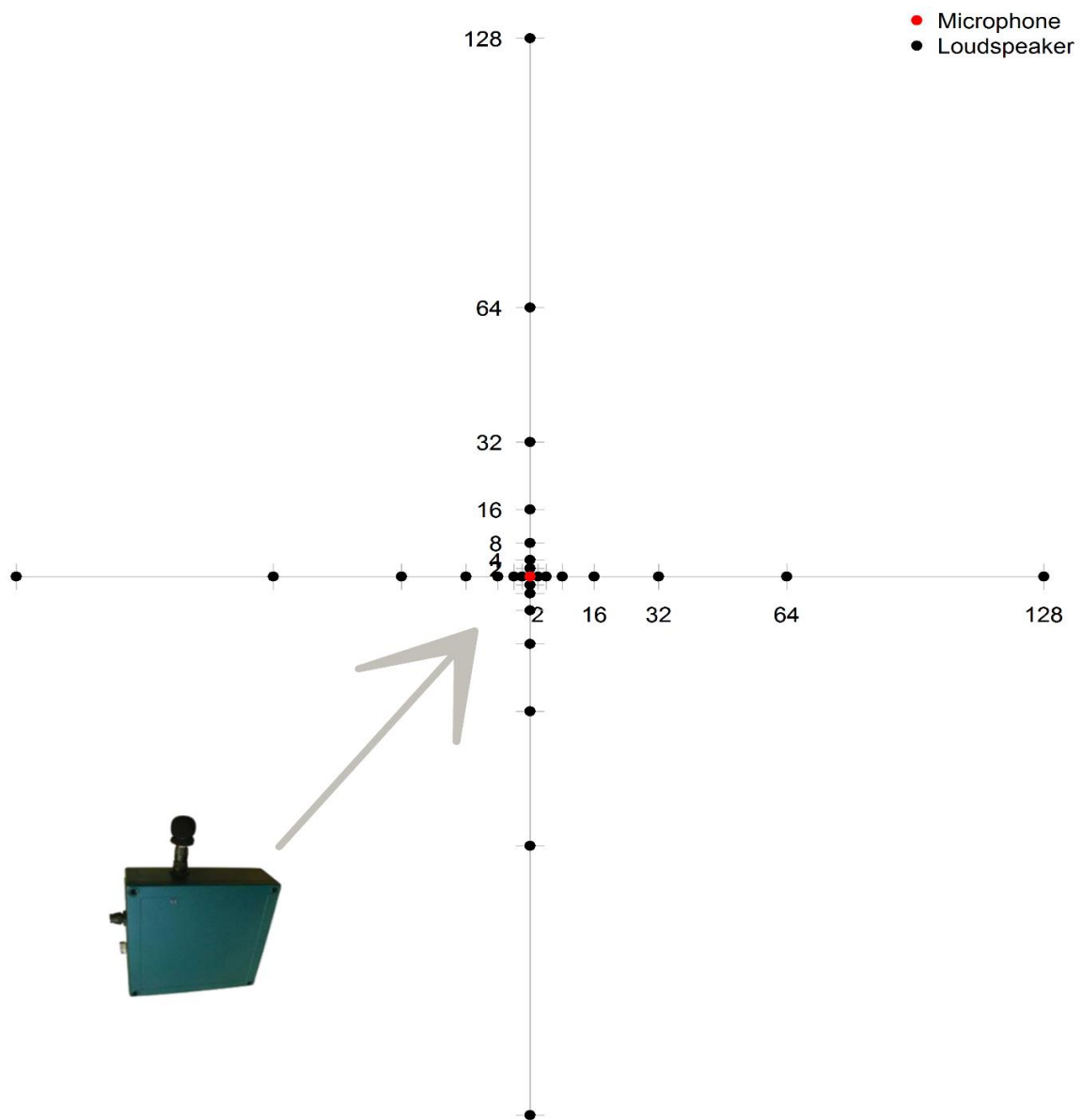


Figure 24: Distances of propagation of the synthesized signal of *P. m. mocinno* in the cloud forest

The microphone was fixed at a starting central point (N 14°32.678'; W 91°11.145') and the loudspeaker was moved away from the starting point to record at six distances. Both microphone and loudspeaker were placed at a similar height of 7 m corresponding to the usual calling height of *P. m. mocinno*. The distances between the loudspeaker and the microphone were set to 1 (control), 4, 8, 16, 32, 64 and 128 m (Figure 24). The geographical coordinates of each playback were taken with a GPS Garmin 64S and the distances between the loudspeaker and the microphone were measured with a Laser meter Leica Disto D8. The ambient temperature and the relative humidity were measured with a Multi Sensor Ermes 01. To evaluate the attenuation of the propagated signals, six sound pressure levels in dB of the synthesized sounds were measured for each vocalization type

at each distance with a sound level meter Testo 815 (fast setting, A scale, 50-100 dB range).

For each distance, the recorded vocalizations were then examined in the time versus amplitude domain on the average envelope of the 15 repetitions of each of the four vocalizations, in the frequency versus amplitude domain on their averaged spectrum, and in the time versus frequency domain on their average frequency modulation measured with a short-time Fourier transform or spectrogram. The averaged parameters were compared at a given propagation distance to those obtained at 1 m (control) by using Pearson's product-moment correlation coefficient for the average envelopes and spectra, and the RV coefficient for the average spectrograms. The analysis was limited to the 500-3500 Hz frequency band corresponding to the bandwidth shared by all the vocalization types. These analyses were run with the R packages *seewave* (Sueur et al, 2008) and *FactoMineR* (Husson et al, 2008).

1.4 Results

1.4.1 Vocalization repertoire

The acoustic activity of *P. m. mocinno* started at dawn at 05:00 h, maintained until mid-day, decreased until 15:00, started again around 16:30 to finish at 18:00 h. The vocal repertoire was made of territorial, alarm, courtship, and contact vocalizations (Figure 25). The results for all the acoustic features of each vocalization are presented in Figure 25.

1.4.1.1 Territorial vocalization

Males emitted territorial vocalizations at dawn and dusk when perched on branches near their nesting sites. The territorial vocalization consisted in syllables made of a pair of alternating notes with different frequency characteristics, one higher (TH) than the other (TL). These alternated notes could be repeated in a series of 2 to 20 syllables. The TH note had a duration of 0.39 ± 0.10 s (0.23-0.62 s). The TH note was characterized by a sliding up-down-up frequency modulated shape, with a peak frequency of 1662.80 ± 89.66 Hz (882.90-1313.50 Hz). The TL had a duration of 0.39 ± 0.11 s (0.17-0.74 s) with a modulated frequency, sliding up to down according an "L" shape and a peak frequency of 1089.70 Hz (820.30-1227.40 Hz). In each series, the syllables were separated by a silence of 0.65 ± 0.17 s.

1.4.1.2 Alarm vocalization

Both sexes produced alarm vocalizations when they were disturbed or when flying from one perch to another. Two or more individuals produced these vocalizations as well when they were close together feeding, for instance, on the same tree.

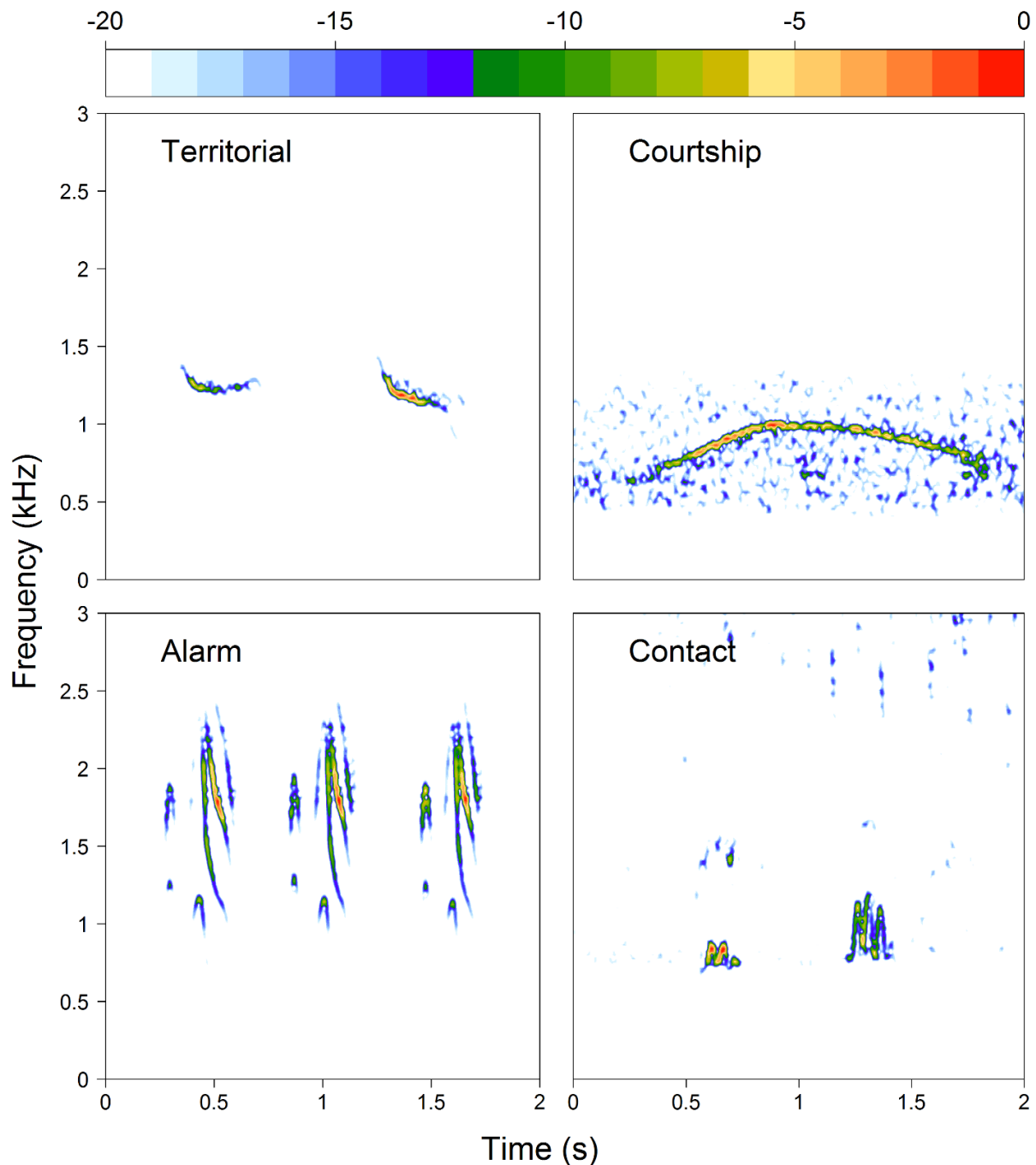


Figure 25: Spectrograms of the four vocalization types of *P. m. mocinno* (short-time Fourier transform parameters: Hann window made of 2048 samples and 87.5% of overlap between consecutive windows)

The alarm vocalization was composed by the repetition of syllables of two notes (note 1 and 2) or sometimes of only one note (note 2). Individuals produced only the second note repeatedly when perched without changing place, moving the tail up and down. The individuals repeated syllables of two notes when they were in higher threat, by the time of changing the perch to another site close to the first perch, or just flying

away, extending the tail feathers fanwise. When composed of two notes, the first note had a duration of 0.07 ± 0.01 s and the second note had a longer duration of 0.29 ± 0.07 s. The first note had a peak frequency of 1298.8 ± 365.83 Hz, and the second note had a peak frequency of 1559.60 ± 365.85 Hz. The two notes were separated by 0.05 ± 0.02 s, and the separation between each pair of notes was 0.25 ± 0.05 s with a time separation inversely proportional to the level of excitation of the individuals, ranging from 0.16 to 0.36 s. The syllable series were particularly fast and composed of 7 to 11 syllables when individuals were flying away.

1.4.1.3 Courtship vocalization

Individuals of both sexes produced a courtship vocalization before the nesting season in January and February. This soft vocalization was emitted when a male was in presence of one or two females and eventually other males (2-4). In this last case, the courtship vocalizations alternate or overlap.

The courtship vocalization consisted of one note with a duration of 1.01 ± 0.37 s and an inverted “V” shape in a narrow frequency band. The peak frequency had an average of 1032.5 ± 342.81 Hz. The minimum and maximum frequencies were 718.9 ± 131.76 Hz and 1168.4 ± 374.91 Hz respectively.

1.4.1.4 Contact vocalization

The contact vocalization was produced by groups feeding on fruits on the same tree (2 to 4 males, and 1 or 2 females). Vocalizing individuals moved from one branch to another while flapping their wings.

The contact vocalization was composed of notes with a fast FM, a duration of 0.26 ± 0.40 s and a peak frequency of 963.1 ± 155.30 Hz. The minimum and maximum frequencies were 694.5 ± 68.95 Hz and 1231 ± 134.04 Hz respectively.

1.4.2 Propagation of the vocalizations of *P. m. mocinno* through the cloud forest

1.4.2.1 Sound pressure level attenuation

The average sound pressure level of the ambient noise was of 31.45 ± 0.92 dB (n= 10). The mean relative humidity was 70.25% and the mean temperature was 17°C.

Table 2: Characteristics of each vocalization type of *P. m. mocinno*. NA: not relevant for this type of vocalization. n: number of individuals (number of notes). TL: note with lower pitch in the syllable. TH: note with higher pitch in the syllable

Mean \pm standard deviation						
Acoustic variables	Territorial TL	Territorial TH	Courtship	Alarm note 1	Alarm note 2	Contact

<i>n</i>	5 (115)	5 (115)	4 (76)	5 (49)	5 (74)	2 (22)
Duration (s)	0.39±0.11 0.1750-0.7430	0.39±0.1 (0.23-0.62)	1.01±0.37 0.27-2.02	0.072±0.014 0.04-0.11	0.29±0.07 0.11-0.44	0.26±0.04 0.19-0.35
Median frequency (Hz)	1078±96.59 818.3-1184.3	1147.6±79.22 904.40-1313.5	1018.9±298.71 624.5-1851.9	1356.6±313.72 882.9-1808.8	1550.8±323.74 947.5-2239.5	949.4±79.16 818.3-1119.7
Peak frequency (Hz)	1089.7±100.04 820.3-1227.4	1148.7±89.66 (882.90-1313.5)	1032.5±342.81 646.0-2088.7	1298.8±365.84 796.7-1938	1559.6±365.85 925.9-2239.5	963.1±155.3 732.1-1335.1
Higher frequency (Hz)	1444±146.58 1151-1788	1398±110.17 1183-1666	1168.4±374.91 673.7-2202.7	1932±615.22 1044-2705	2854±581.72 1121-4170	1231±134.04 908.5-1455.9
Lower frequency (Hz)	788.5±70.57 649.7-1076.3	964.5±147.21 740.1-1229	718.9±131.77 411.4-1022.3	628.7±114.65 426.8-838.2	561.1±115.9 337.9-790.4	694.5±68.95 551.2-791.5
Inter quartile range (Hz)	92.77±72.59 21.5-304.7	83.9±75.91 21.5-366.1	172.8±144.42 21.5-732.1	333.40±275.4 43.1-861.3	491.90±201.99 129.2-947.5	193.8±70 43.1-344.5
First quartile frequency (Hz)	1033.70±101.74 775.2-1162.8	1099.7±93.87 867.2-1292	914.6±233.26 559.9-1636.5	1161.20±285.88 796.7-1744.2	1332.2±305.09 818.3-2131.8	859.4±65.76 732.1-947.1
Third quartile frequency (Hz)	1126.4±88.1 861.3-1248.9	1183.6±78.22 990.5-1335.1	1087.4±336.24 646-2067.2	1496.6±324.68 925.9-1851.9	1825±231.54 1012-2347	1053.2±117.16 818.3-1292
Inter note duration (s)	0.65±0.17 (0.29-0.99)		NA	0.05±0.02 0.002-0.14		NA
Inter syllable duration (s)	9.69±6.92 (1.58-33.19)		NA	0.25±0.05 0.16-0.36		NA

Among the four vocalizations, the contact vocalization was the most attenuated with distance to the source, then the courtship and the less attenuated were the territorial and alarm vocalizations. At 128 m, the level in dB of the contact vocalization was below the background noise. At this same distance, the courtship vocalization had almost the same dB value as the background noise and the territorial and alarm vocalizations had a dB value just above it. The results of attenuation by vocalization at all the distances are presented in Table 3 and Figure 26.

1.4.2.2 Modification of the amplitude envelope

The amplitude envelope of the courtship vocalization was the most modified with distance to the sound source, among the four types of vocalizations. The less modified were the territorial and alarm vocalizations, both composed of syllables of two different notes, one higher in pitch than the other. The amplitude envelope of the higher pitched note (note 1) of the alarm vocalization was more modified with distance than the lower pitched note (note 2). The results for all distances are presented in Table 4 and Figure 7.

Table 3: Attenuation in sound pressure level (dB) of the vocalizations of *P. m. mocinno* according to the distance from the source. < BN indicates that the sound pressure level value was below the background noise

Distance (m)	Territorial (dB)	Alarm (dB)	Courtship (dB)	Contact (dB)
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4	70.73	70.63	57.51	47.17
8	68.29	70.82	55.02	49.80
16	55.85	59.32	49.68	43.25
32	57.33	54.01	46.47	39.00
64	47.29	46.39	38.00	36.68
128	33.65	35.93	< BN	< BN

1.4.2.3 Modification of the frequency spectrum

The most modified frequency spectra according to propagation distance were those of the contact and courtship vocalizations, with a high degradation at 128 m. The less degraded frequency spectrum was the one of the territorial vocalization, and then of the alarm vocalization. The results for all distances from the source are presented in Table 4 and Figure 7.

1.4.2.4 Modification of the frequency modulation

The most modified frequency modulation was that of the second note (high pitch) of the alarm vocalization. The most resistant frequency modulation was that of the TL note of the territorial vocalization (low pitch). The results of RV coefficients for all distances are presented in Table 4 and Figure 7.

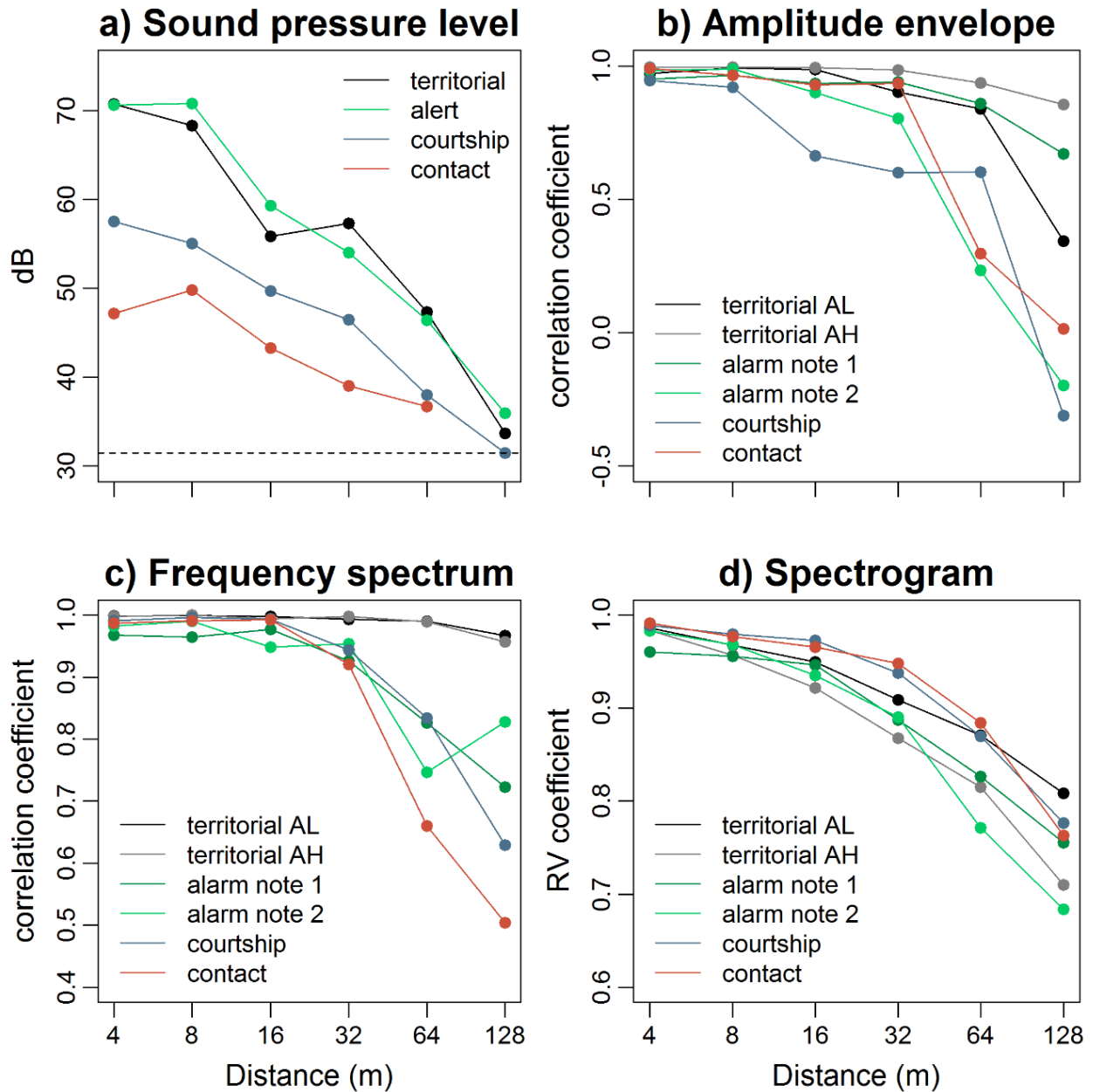


Figure 26: Modification of the vocalizations of *P. mocinno* by distance of propagation. a) Sound pressure level, b) Amplitude envelope, c) Frequency spectrum, d) Spectrogram

Table 4: Correlation coefficients of amplitude envelopes, frequency spectra and frequency modulations between signals recorded at 1 m (control) and signals at 4, 8, 32, 64 and 128 m

Direction	Distance (m)	Territorial TL	Territorial TH	Alarm note 1	Alarm note 2	Courtship	Contact
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	4	0.97	1.00	0.95	0.98	0.95	0.99
	8	0.99	1.00	0.97	0.99	0.92	0.97
Amplitude envelope	16	0.99	0.99	0.94	0.90	0.66	0.93
Pearson's coefficient	32	0.90	0.99	0.94	0.80	0.60	0.93
	64	0.84	0.94	0.86	0.23	0.60	0.30
	128	0.34	0.86	0.67	-0.20	-0.31	0.01
	4	1.00	1.00	0.97	0.98	0.99	0.99
	8	1.00	1.00	0.96	0.99	1.00	0.99
Frequency spectrum	16	1.00	0.99	0.98	0.95	0.99	0.99
Pearson's coefficient	32	0.99	1.00	0.93	0.95	0.94	0.92
	64	0.99	0.99	0.83	0.75	0.83	0.66
	128	0.97	0.96	0.72	0.83	0.63	0.50
	4	0.99	0.98	0.96	0.98	0.99	0.99
	8	0.97	0.96	0.96	0.97	0.98	0.98
Frequency modulation	16	0.95	0.92	0.95	0.94	0.97	0.97
RV coefficient	32	0.91	0.87	0.89	0.89	0.94	0.95
	64	0.87	0.82	0.83	0.77	0.87	0.88
	128	0.81	0.71	0.76	0.68	0.78	0.76

1.5 Discussion

Through a detailed acoustic analysis, we characterized four vocalizations constituting the repertoire of the Resplendent Quetzal, *P. mocinno*: the territorial, alarm, courtship and contact vocalizations. These signals differ in their structure and consequently are more or less adapted to propagation at distance.

According to the habitat structure and weather conditions, some sound signals propagate at longer distance than others (Brown et al, 2006; Catchpole & Slater, 2008). In closed habitats, vegetation causes additional attenuation of sound, specifically for the higher frequencies (Evans & Bazley, 1956). *P. m. mocinno* produces vocalizations in the range of 561 to 2854 Hz, a relatively low frequency-band compared to the range of 2000 to 3000 Hz of most bird species (Catchpole & Slater, 2008). High humidity enhances transmission of sound and the effect of humidity varies both with ambient temperature and frequency (Evans & Bazley, 1956). With a relative humidity higher than 20%, as usual in cloud forests, the greatest attenuation of sound happens at temperatures below 0° (Harris, 1966). In our propagation experiments, the mean relative humidity was 70.25 % and the mean temperature was 17°C, the vocalizations of *P. mocinno* are therefore weakly attenuated by these factors during propagation in the cloud forest.

The territorial vocalization of *P. m. mocinno* consists of a repetition of syllables composed of two notes which are weakly degraded by distance through the cloud forest.

We only detected a significant degradation of the amplitude modulation (AM) at a distance of 128 m, the frequency spectrum of the signal being still well preserved. This suggests that potential receivers, as females or competing males, could infer information about the sender at a relatively long distance.

We identified an alarm vocalization produced by both sexes of *P. m. mocinno*. The alarm vocalization of *P. m. mocinno* consists of sequences of syllables composed by two notes, one short note followed by a longer note with a broader bandwidth and higher frequency than the first. As for other bird species, the structure of alarm vocalizations of *P. m. mocinno* can vary gradually with the urgency of the threat and even provide functionally referential information (Brown et al, 2006). The amplitude modulation (AM) of this vocalization degraded significantly only from 64 m, as well as the frequency spectrum. We infer that this vocalization is intended for mid to long range communication.

Courtship signals of birds provide information on male motivation and quality, and females use this information for pairing and mating decisions (Brown et al, 2006). The courtship vocalizations of *P. m. mocinno* are discreet signals, with a slow FM in a narrow frequency band. According to the propagation experiment, the courtship vocalization was clearly more attenuated with distance than the alarm and territorial vocalizations. This signal seems adapted to convey “private” information, when males and females are in close vicinity. In particular, the amplitude envelope of the courtship vocalization was highly degraded by distance, while the frequency modulation was more resistant. *P. m. mocinno* is known to be a monogamous species (Solórzano & Oyama, 2009) and courtship vocalizations might allow mate recognition from one year to the next. Individual identity parameters being supported by vocalization features susceptible to degradation during propagation (Mathevon et al, 2008), the frequency modulation of *P. mocinno* courtship vocalization could be important for mate recognition. The frequency of the courtship vocalization of *P. mocinno* is relatively low. High-frequency sounds, which can bounce off objects and leave a marked sound shadow, are more localizable than low frequency sounds and so are more likely to stimulate the two ears equally (Catchpole & Slater, 2008). Therefore the soft courtship vocalization of *P. mocinno* seems adapted to short range communication and could be difficult to localize by potential predators.

The contact vocalization of *P. m. mocinno* consists in a repeated fast modulated note with a lowest frequency and amplitude compared to the three other vocalization types. The fast FM of the note is particularly susceptible to be blurred by reverberation on obstacles (Brown et al, 2006) and its weak amplitude level of emission may impair a transmission of information at long range. Like the courtship vocalization, the contact

vocalization seems adapted to a communication at a very short range, for instance when individuals are feeding on the same tree.

The present study provides the first description of the vocalizations of *P. mocinno* showing their capabilities to propagate in the cloud forest, according to their structure and their behavioral context. We have shown that the different vocalizations differ on the basis of their acoustic structure with repeated loud territorial and alarm vocalizations intended for long range, or public communication, and soft courtship and contact vocalizations for short range, or private communication.

1.6 Acknowledgements

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**Chapter 2: Vocalizations of the rare and
flagship species *Pharomachrus mocinno* (Aves:
Trogonidae): implications for its taxonomy,
evolution and conservation**



Tree ferns in Los Andes reserve (picture: Pablo Bolaños)

2.1 Summary

2.1.1 Context

The Resplendent Quetzal *Pharomachrus mocinno* is a rare Neotropical bird included in the IUCN red list of threatened species. Fragmentation of its habitat, the cloud forest, is considered as its main threat. Two subspecies are currently recognized but genetic and morphometric studies suggested they could be considered as full species.

2.1.2 Problematics

We assessed whether male vocalizations would support a species delimitation hypothesis.

2.1.3 Methods

We recorded in the field and downloaded from sound archives vocalizations of 57 individuals from 30 different localities distributed in 11 countries. We estimated the potential acoustic differences of all the *Pharomachrus* taxa with multivariate analyses.

2.1.4 Main results

Our results show vocal differences between *P. m. mocinno* and *P. m. costaricensis* that we argue have a genetic basis, potentially due to genetic drifts developed during the more than three million years of separation between *P. m. mocinno* (from Mexico to Nicaragua) and *P. m. costaricensis* (Costa Rica and Panama). We therefore suggest that *P. mocinno* should be divided into two species.

2.1.5 Perspectives

The elevation to species level has important consequences for the conservation status of the Resplendent Quetzals and redirects conservation efforts for these species. The results of this study could be supported by playback and breeding experiments.

2.1.6 Related communications and publications

Bolaños, P., Sueur, J., Fuchs, J., Aubin, T. (*in revision*). Vocalizations of the rare and flagship species *Pharomachrus mocinno* (Aves: Trogonidae): implications for its taxonomy, evolution and conservation. *Bioacoustics*.

Vocalizations of a flagship bird species (*Pharomachrus mocinno*): implications for conservation status. Bolaños, P., Aubin, T., Sueur, J., Oral presentation at the International Bioacoustics Congress, 2018. Haridwar, India.

2.2 Introduction

The biological species concept is the main evolutionary concept considered to draw the lists of threatened species by the International Union for the Conservation of Nature Red List (IUCN 2001) which are mainly used to rule out national and international policy for nature conservation (Isaac et al. 2004). The species level bears a particular importance for flagship species which act as symbols and attract public interest (Simberloff 1998). Most flagship species are large mammals such as the African elephant (*Loxodonta africana*) for African savannah, the giant panda (*Ailuropoda melanoleuca*) for Chinese bamboo forest, the Bengal tiger (*Panthera tigris*) for Indian forest, the koala (*Phascolarctos cinereus*) for Australian eucalypt woodlands, or the humpback whale (*Megaptera novaeangliae*) for oceans (Courchamp et al. 2018; Groom et al. 2006). Bird species are more rarely used as a nature icon. One exception is the Resplendent Quetzal, *Pharomachrus mocinno* (De la Llave 1832) (Aves: Trogonidae), a rare Neotropical bird harbouring highly coloured, bright and elongated feathers (LaBastille et al. 1972) and regarded as a symbol of Central American cloud forest. The Resplendent Quetzal is the centre of the Guatemalan heritage since Mayan civilizations, being represented in all sorts of arts, drawn on the national flag, and used as the currency name (Bowes and Allen 1969). In addition to its social influence, the Resplendent Quetzal plays a significant ecological role by dispersing the seeds of at least 32 tree species and by participating to the dynamics and resilience of the cloud forest (Solórzano et al. 2000). *Pharomachrus mocinno* is included in the Near Threatened category of the IUCN Red List (Birdlife International 2016) and it is listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora Appendix I of the most endangered species (UNEP-WCMC (Comps.) 2014). The distribution of the Resplendent Quetzal shows an insular pattern limited to well preserved cloud forests in the south of Mexico, Guatemala, El Salvador, Nicaragua, Honduras, Costa Rica and Panama (Solórzano et al. 2003).

Pharomachrus mocinno was originally described by the Mexican naturalist Pablo de la Llave from specimens collected between 1787 and 1803 in Guatemala ('Goatemala') by the Royal Botanical Expedition to New Spain (De la Llave 1832). The name of the specific epithet, *mocinno*, was dedicated to the naturalist José Mariano Mociño, who participated to the expedition, and the genus name referred to the main body characteristics of the bird, *pharos* meaning mantle and *makros* meaning long in ancient Greek. In 1869, the German ornithologist Jean-Louis Cabanis revealed that male specimens from Costa-Rica were smaller than male specimens from Guatemala, motivating the creation of a new subspecies named *P. m. costaricensis* (Cabanis 1869).

This subspecies distinction still persists with the populations of south Mexico, Guatemala, Honduras, El Salvador and Nicaragua classified as *P. m. mocinno* and the populations of Costa Rica and Panama classified as *P. m. costaricensis* (Birdlife International 2016). The distribution areas of the two subspecies are separated by the Nicaraguan depression, a 50 km wide, 600 km long lowland that contains the two largest lakes from Central America, namely Lake Nicaragua and Lake Managua (Marshall 2007). The age of this barrier, which is also known as the biological border region of Nicaragua (Weyl 1980), is not precisely established but arose between the early Pliocene (5 million years ago) and the beginning of the Pleistocene (1.8 million years ago), probably when the Panamanian Isthmus was formed three million years ago (Keigwin 1982; Solórzano et al. 2004). Phylogenetic analyses revealed two monophyletic groups, corresponding to each subspecies for which gene flow was possibly interrupted for three to six million years corresponding to the age of the Nicaraguan depression (Solórzano and Oyama 2009). The lack of current contact between the populations of the two subspecies has also been evidenced by telemetry studies, showing that individuals of *P. m. costaricensis* from Costa Rica had no contact with populations of *P. m. mocinno* from north Nicaragua (Powell and Bjork 1995).

Taking taxonomic decisions based on the “amount of genetic difference” as an absolute criterion for deciding whether two operational taxonomic units are distinct species, is not recommended (McDonough et al. 2008). Ideally to test the taxonomic status of candidate populations for specieshood, genetic evidence should be supported by complementary character evidences (Cotterill et al. 2014). Supporting the original observations of Jean-Louis Cabanis (1869), recent morphometry analyses revealed differences in size between the two subspecies, *P. m. mocinno* being larger than *P. m. costaricensis*, and having longer wings, a wider bill, a longer tarsus and longer and wider tail cover feathers for the male (Schulz and Eisermann 2017; Solorzano et al. 2009). Behavioural characters, like geographic variation in songs and calls, are also of significant importance for species differentiation (Wei et al. 2015). Apart from the oscine passerines, hummingbirds and parrots, there are no evidence that other birds could learn their vocalizations (Kroodsma and Konishi 1991). The species *P. m. mocinno*, as non-passerine bird, would not acquire its vocalizations through learning processes and therefore would not be subject to cultural evolution (Wei et al. 2015). Thus, the acoustic differences between populations, if they exist, could be mainly related to genetic factors (Brown and Lemon 1979). Surprisingly, no comparison between the sounds produced by the two subspecies has been documented yet.

To tackle the subspecies vs species taxonomy (Solórzano and Oyama 2009), we conducted an acoustic comparison between the two subspecies *P. m. mocinno* and *P. m.*

costaricensis and between all *Pharomachrus* taxa based on multivariate analyses and machine learning techniques. Our analyses show that the acoustic signals of *P. m. mocinno* and *P. m. costaricensis* differ enough to support the elevation of this two subspecies to species rank. We then discuss the consequences of this taxonomy change in terms of evolution and conservation.

2.3 Material and methods

2.3.1 Acoustic analysis

To assess the acoustic specificity of *P. m. mocinno* and *P. m. costaricensis*, the territorial vocalization of the two subspecies were compared with each other, and with the territorial vocalization of the four other closely related species *P. antisianus*, *P. auriceps*, *P. fulgidus* and *P. pavoninus*. The territorial song was the only vocalization selected for this comparison due to a clear functional and structural acoustic homology between species in the family Trogonidae. The territorial song mainly consists of multiple repetitions of a two-note syllable at fairly regular intervals, with little change in pitch (Johnsgard 2000). The territorial song has been already used to make comparisons between species in the family (Ornelas et al. 2009).

Seven males of *P. m. mocinno* were visually localized and recorded in January and February 2016 and 2017 during the peak of vocal activity in two protected areas of Guatemala: the “Refugio del Quetzal”, San Marcos (N 14° 56' - W 91° 52', 1531 m) and “Los Andes”, Suchitepéquez private reserve (14° 32' - 91° 11', 1992 m). Recordings were realized with a Tascam digital recorder DR-100 MK II (44.1 kHz sampling frequency, dynamic range of 16 bit) connected to a Sennheiser ME-67 directional microphone (frequency response: 40-20000 Hz \pm 2.5 dB). To increase the number of individuals and include other sites and the closely related species, recordings of 50 individuals available in five sound libraries (Xeno-Canto, Macaulay Library, Biblioteca de Sonidos de Aves de México, Laboratorio de Bioacústica de la Universidad de Costa Rica, and Borror Laboratory of Bioacoustics) were included in the analysis, collected in different locations and/or on different dates, or alternatively when the sound recordists specified that the vocalizations belonged to different individuals. When the libraries provided sounds in compressed mp3 format that are not ideal for sound analysis in birds (Araya-Salas et al. 2017), recordings were systematically requested to the authors in wav format with a minimum sampling rate of 44.1 kHz and a dynamic range of 16 bit. A total of 57 individual recordings (*P. m. mocinno*, n=21; *P. m. costaricensis*, n= 15; *P. antisianus*, n=7; *P. auriceps*, n=6; *P. fulgidus* n=4; *P. pavoninus* n=4) from 30 different localities distributed

in 11 countries (Mexico, Guatemala, Honduras, Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru, Bolivia and Brazil) could be analyzed (Figure 27, Annexes Table S1).



Figure 27: Map of Central America and north of South America showing the sites of recordings of *Pharomachrus* species and subspecies used for the comparative analysis (Google® background). Picture of *P. m. mocinno*, approximate body length 41 cm (picture reproduced with the authorization of Ricky Lopez)

The vocalizations were analysed with Raven Pro 1.4 software (www.birds.cornell.edu/raven) directly from on-screen measurement cursors on the oscillogram for time parameters (time precision = 0.0232 s) and on the spectrogram for frequency parameters (frequency precision = 21.5 Hz). Taking measurements on the spectrogram might not be optimal due to limited time and frequency precisions when

proceeding formal description of vocalizations, but is valuable when doing comparison between sounds when only relative differences matter. The parameters for each of the two successive notes, note 1 and note 2, composing the syllable were: note duration (s), inter-note separation (s), peak frequency that is the frequency of highest energy (Hz), centre frequency (Hz), highest and lowest frequencies (Hz), first and third frequency quartiles (Hz) (the frequencies that divide the selection into frequency intervals containing respectively 25% and 75% of the energy), frequency inter-quartile-range (difference between the first and third frequency quartiles). The inter-syllable separation (s) was also measured. In addition, the frequency modulation (FM) of each note was assessed by measuring the dominant frequency in a series of 20 frequency measurements equally distributed in time along each note using the package *seewave* 2.0.5 (Sueur et al. 2008) from the R 3.2.5 environment (Development Core Team 2008). The first mathematical derivative of these time series was computed, and the resulting positive and negative values were summed to obtain the positive and negative FM respectively. The FM was then characterized by two features, the positive and negative FMs. In total, a matrix of 57 individuals by 22 variables was obtained (one temporal parameter, seven frequency parameters, two FM parameters per note, one temporal parameter between notes, and one temporal parameter between syllables) (Figure 28).

As the number of notes found for each individual varied from 12 to 639, a random subsample of 40 notes was applied for the individuals that produced more than 40 notes to ensure balanced datasets. A total of 1738 notes were analysed. For each note, the average of each parameter per individual was calculated. The spectrograms were made with *seewave* with a Fourier transform made of 2048 samples tapered with a Hanning window and with an overlap of 87.5%.

To test how the 22 acoustic features could classify correctly *P. m. mocinno*, *P. m. costaricensis* and the closely related species, two supervised classification methods used in machine learning were applied, namely a multiclass linear discriminant analysis (LDA) for the subspecies comparison (Fisher 1936) and a balanced random forest analysis (RF) (Breiman 2001) including the subspecies and the other *Pharomachrus* species.

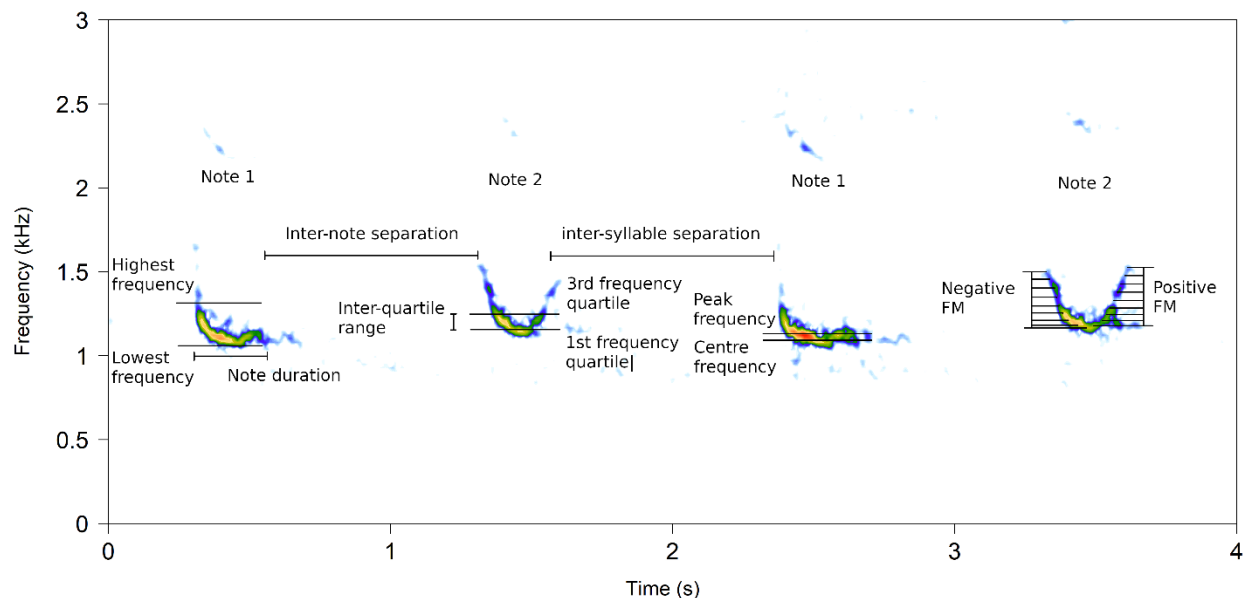


Figure 28: Annotated spectrogram of a male territorial vocalization of *P. m. mocinno*, showing the time and frequency measurements (short-time Fourier transform parameters: Hann window made of 2048 samples and 87.5% of overlap between successive windows)

For the LDA, the data were first Z-transformed and reduced to two dimensions with a principal component analysis (PCA). The coordinates of the recordings according to the first two PCA axes were used as input data for the LDA. The taxa names were used as an explained (dependent) variable so that the LDA classified the recordings according to subspecies. A LDA confusion matrix was built to estimate the percentage of correct classification, and PCA scores were plotted as a function of latitude to test whether the territorial vocalizations of *P. m. mocinno* and *P. m. costaricensis* intergrade along their distribution. Both PCA and LDA analyses were carried out with the R package *ade4* (Dray et al. 2016).

For the RF, a Breiman's RF algorithm was applied on the 57 by 22 matrix with the help of the *randomForest* R package (Liaw and Wiener 2015). The RF analysis was designed so that the six *Pharomachrus* taxa were defined as the explained (dependent) variable and the 22 acoustic features as the explaining (independent) variables. A total of 4000 decision trees was built based on a random sample with replacement among 63% of the observations. A confusion matrix was built with an average error rate based on the observations not sampled, known as the out-of-bag observations. The relative importance of the explaining variables, *i.e.* of the acoustic features, was calculated using the Gini index. If the variable is useful, it tends to split mixed labelled nodes into pure single class nodes, then the importance of the explained variables is explained by this index.

A Chi-square test was conducted to evaluate if the number of individuals classified by the LDA or the RF was significantly higher than a classification expected by chance.

2.3.2 Molecular analyses

The 255 bp of the mitochondrial Control Region, of the 16 individuals of *P. m. mocinno* and 9 individuals of *P. m. costaricensis*, published by Solórzano *et al.* (2004), were reanalysed using other statistics (Da, dxy, uncorrected sequence divergence) classically used to assess genetic differentiation between two lineages. All analyses were performed in DNAsp 6.0 (Rozas *et al.* 2017).

2.4 Results

Spectrograms of the typical territorial vocalizations of each *Pharomachrus* taxa are compared in Figure 29. The first two axes of the PCA, which explained 61.17% of the total variance, showed a separation between *P. m. mocinno* and *P. m. costaricensis* (Figure 30). Plotting the PCA scores with respect to latitude does not indicate that the territorial song intergrades, suggesting that there is no clinal variation in vocalizations over the study scales (Figure 31). The LDA obtained from the PCA scores showed a clear differentiation between *P. m. mocinno* and *P. m. costaricensis*. The confusion matrix returned 89.88% of correct classification (*P. m. mocinno* 19 of 21 individuals assigned correctly, *P. m. costaricensis* 13 of 15 individuals assigned correctly), and exceeded classification expected by chance (Chi-square test, d.f.=1, $\chi^2=18.37$, $p < 0.001$) (Table 5). The acoustic features of the two subspecies of *Pharomachrus* are shown in Table 6.

The RF classification showed that the most important acoustic features to classify the *Pharomachrus* taxa were the peak and centre frequency of the second note, followed by the centre frequency of the second and first note (Figure 32). These parameters are followed by the third frequency quartile of the second and first notes, then the inter-syllable and inter-note separation, the duration of the first note, the frequency inter-quartile of the second note, the peak frequency of the first note and the duration of the second note. The lowest and highest frequencies, the negative and positive FM, and the frequency inter-quartile range of the two notes, did not appear as major discriminating parameters.

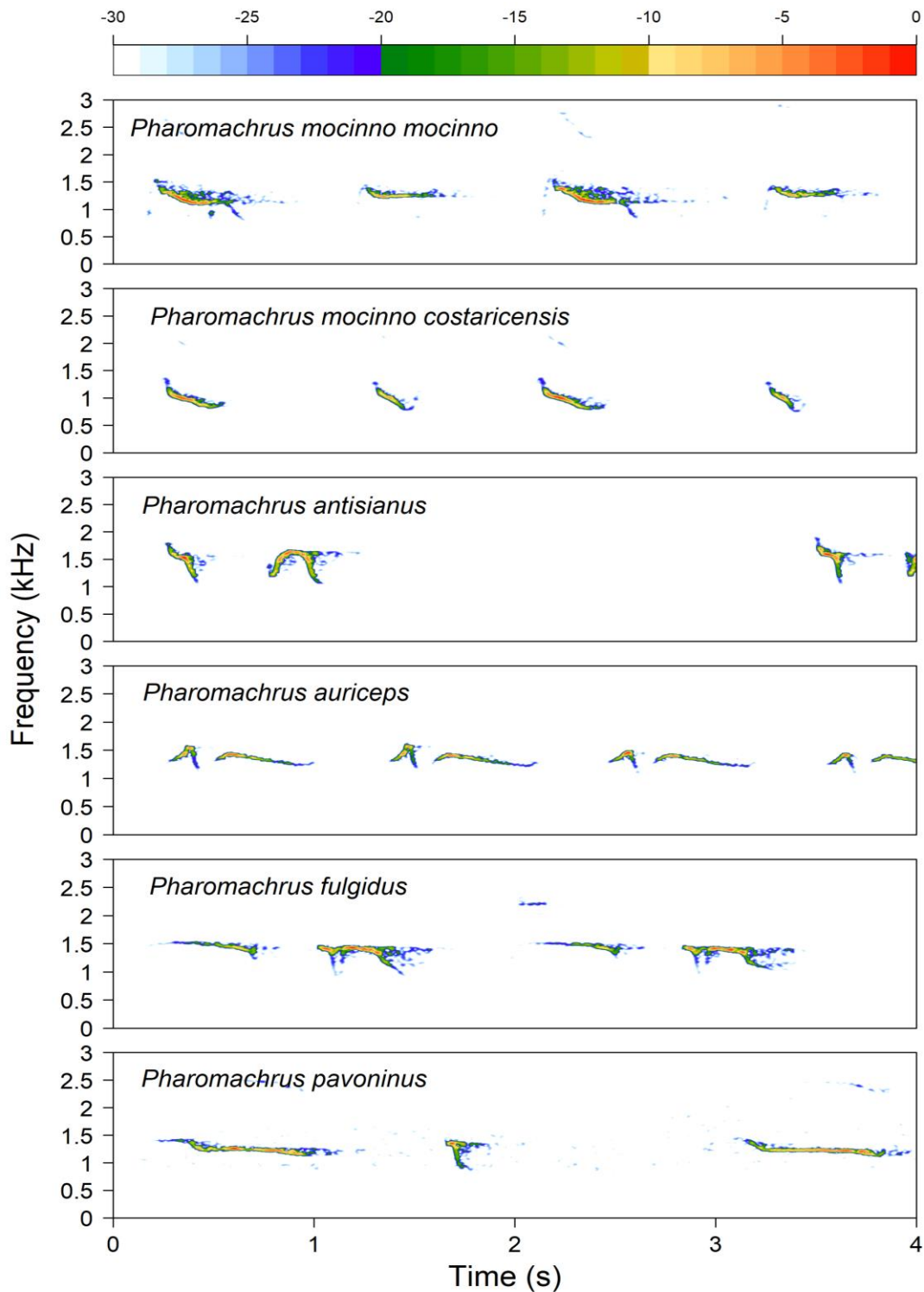


Figure 29: Spectrograms of the territorial vocalizations of *P. m. mocinno*, *P. m. costaricensis*, *P. antisianus*, *P. auriceps*, *P. fulgidus* and *P. pavoninus* (short-time Fourier transform parameters: Hann window made of 2048 samples and 87.5% of overlap between successive windows). The vocalizations were aligned to fit into a 4 s window to allow temporal comparison

Table 5: LDA confusion matrix used to classify the species belonging to *P. m. mocinno* or *P. m. costaricensis*, based on 22 acoustic measurements of the territorial vocalizations (21 individuals for *P. m. mocinno* and 15 individuals for *P. m. costaricensis*)

	<i>P. m. mocinno</i>	<i>P. m. costaricensis</i>
<i>P. m. mocinno</i>	92.86	0.07
<i>P. m. costaricensis</i>	13.1	86.9

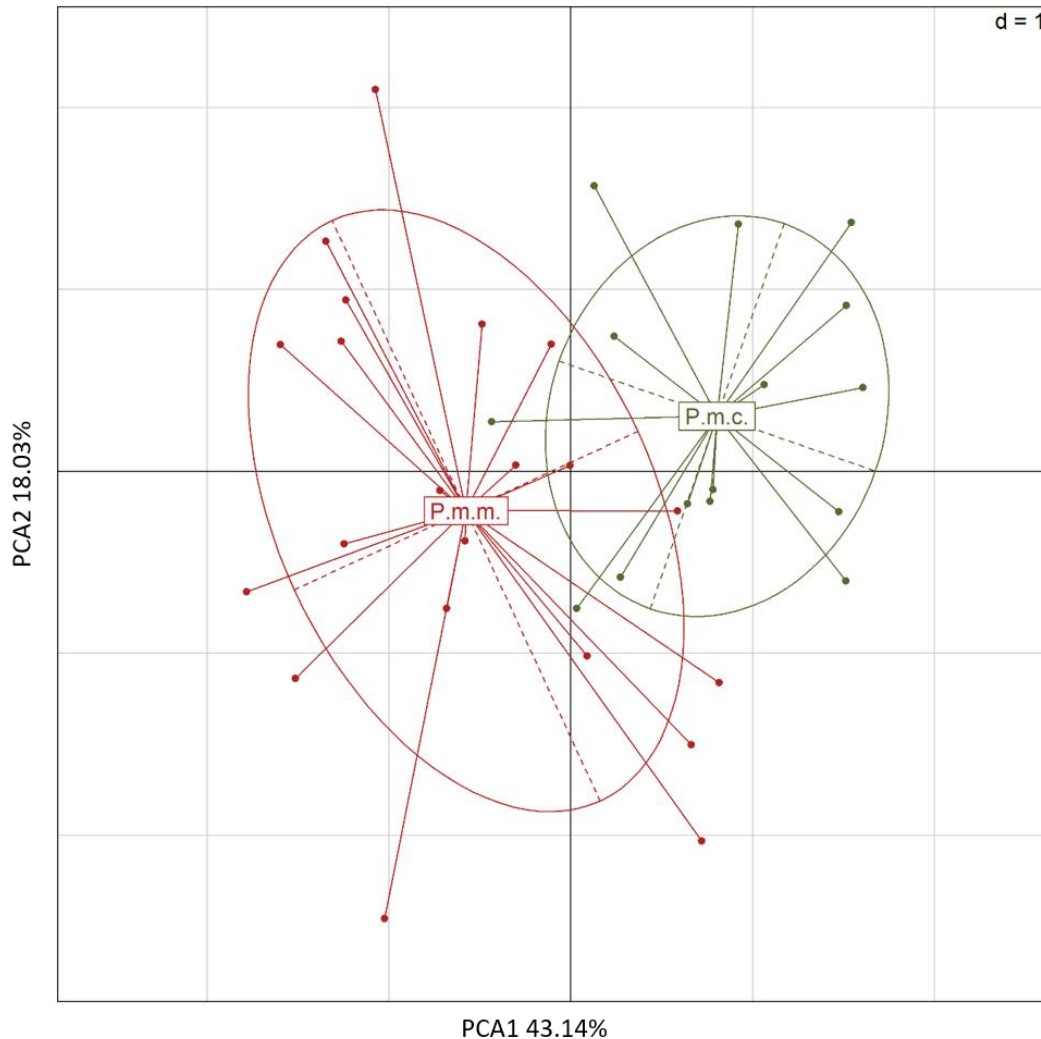


Figure 30: Principal Component Analysis (PCA) projection showing the space defined by the two first principal axes that explained 61.17% of the total variance. Each point corresponds to a single individual. *Pharomachrus mocinno mocinno* (P.m.m.) individuals are indicated in red and *P. m. costaricensis* (P.m.c.) individuals in green. The ellipses surround the centroid of each taxa and delimit 67% of the vocalizations that are expected to be associated with each taxa

Table 6: Characteristics of the territorial vocalization of *P. m. mocinno* and *P. m. costaricensis* (21 individuals for *P. m. mocinno* and 15 individuals for *P. m. costaricensis*). Mean \pm SD (range)

Acoustic Feature	<i>P. m. mocinno</i>	<i>P. m. costaricensis</i>
Inter note separation (s)	0.53 \pm 0.12 (0.08-0.65)	0.63 \pm 0.12 (0.41-0.82)
Inter syllable separation (s)	0.68 \pm 0.16 (0.38-1.01)	0.6 \pm 0.09 (0.4-0.73)
Note 1		
Duration (s)	0.38 \pm 0.09 (0.27-0.59)	0.3 \pm 0.05 (0.23-0.39)
Center frequency (Hz)	1094.8 \pm 99.4 (880.7-1205.9)	986.1 \pm 82.87 (865.9-1094.6)
Highest frequency (Hz)	1462 \pm 140.53 (1190-1728)	1409 \pm 182.28 (1147-1771)
Lowest frequency (Hz)	910.7 \pm 145.19 (678.8-1106)	723.6 \pm 65.75 (613-853.7)
First frequency quartile (Hz)	1051.5 \pm 102.98 (835.9-1169.1)	933.3 \pm 84.03 (816.5-1061.1)
Third frequency quartile (Hz)	1143.2 \pm 81.61 (954.3-1255.3)	1035.2 \pm 77.02 (905.6-1131.7)
Inter-quartile range (Hz)	91.76 \pm 55.9 (32.29-278.62)	101.88 \pm 40.22 (56.24-193.80)
Peak frequency (Hz)	1098 \pm 95.66 (889.3-1210.9)	991.4 \pm 84.23 (867-1109)
Negative FM (Hz)	1.65 \pm 0.43 (0.83-2.53)	1.5 \pm 0.33 (0.98-1.99)
Positive FM (Hz)	1.61 \pm 0.42 (0.95-2.49)	1.48 \pm 0.29 (1.03-1.99)
Note 2		
Duration (s)	0.34 \pm 0.09 (0.18-0.52)	0.31 \pm 0.06 (0.22-0.43)
Center frequency (Hz)	1164 \pm 84.66 (1006-1343)	987.6 \pm 67.21 (893.6-1100.5)
Highest frequency (Hz)	1439 \pm 129.81 (1212-1643)	1324 \pm 131.78 (1154-1679)
Lowest frequency (Hz)	970.8 \pm 135.94 (731.2-1196.5)	774.9 \pm 68.65 (689.7-913.3)
First frequency quartile (Hz)	1115.5 \pm 100.73 (943.9-1319.7)	931.2 \pm 81.95 (802.1-1065.3)
Third frequency quartile (Hz)	1210 \pm 81.61 (1072-1366)	1046.2 \pm 77.02 (970.3-1134.1)
Inter-quartile range (Hz)	94.55 \pm 55.91 (30.88-343.56)	114.95 \pm 40.22 (37.49-199.95)
Peak frequency (Hz)	1168 \pm 81.47 (1036-1354)	992.8 \pm 68.29 (881.2-1108.4)
Negative FM (Hz)	1.64 \pm 0.49 (0.63-2.53)	1.54 \pm 0.32 (1.01-2.1)
Positive FM (Hz)	1.66 \pm 0.49 (0.66-2.6)	1.54 \pm 0.3 (1.13-2.1)

The confusion matrix built on the balanced RF classification revealed a high correct classification rate for all the species and subspecies with 81.9 % for *P. m. mocinno* (17 of 21 individuals assigned correctly, 86.67% for *P. m. costaricensis* (13 of 15 individuals assigned correctly), 100% for *P. antisianus* (7 of 7 individuals assigned correctly), 100% for *P. auriceps* (6 of 6 individuals assigned correctly), 75% for *P. fulgidus* (3 of 4 individuals assigned correctly), and 100% for *P. pavoninus* (4 of 4 individuals assigned correctly) (Table 7), all rates exceeded classification expected by chance (Chi-square test, d.f.=25, $\chi^2=221.1$, $p < 0.001$)

Table 7: RF confusion matrix used to classify the species belonging to *Pharomachrus* genus (total individuals is 21 for *P. m. mocinno*, 15 for *P. m. costaricensis*, 7 for *P. antisianus*, 6 for *P. auriceps*, 4 for *P. fulgidus*, 4 for *P. pavoninus*) on the basis of 22 acoustic features. Data mentioned in the text is underlined

	<i>P. m. mocinno</i>	<i>P. m. costaricensis</i>	<i>P. antisianus</i>	<i>P. auriceps</i>	<i>P. fulgidus</i>	<i>P. pavoninus</i>	Class error
<i>P. m. mocinno</i>	<u>80.95</u>	14.29	0.00	0.00	4.76	0.00	0.19
<i>P. m. costaricensis</i>	13.33	<u>86.67</u>	0.00	0.00	0.00	0.00	0.13
<i>P. antisianus</i>	0.00	0.00	<u>100.00</u>	0.00	0.00	0.00	0.00
<i>P. auriceps</i>	0.00	0.00	0.00	<u>100.00</u>	0.00	0.00	0.00
<i>P. fulgidus</i>	25.00	0.00	0.00	0.00	<u>75.00</u>	0.00	0.25
<i>P. pavoninus</i>	0.00	0.00	0.00	0.00	0.00	<u>100.00</u>	0.00

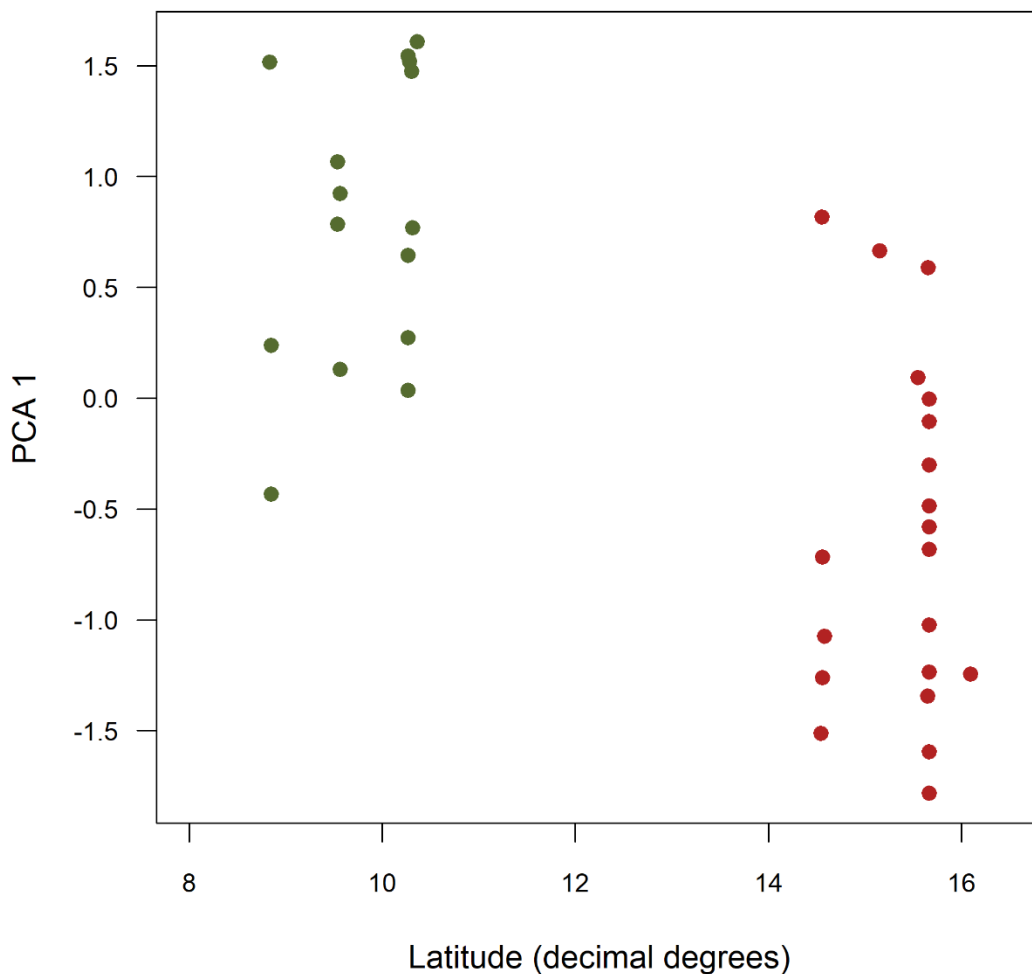


Figure 31: Scores obtained from principal component analysis (PCA) based on 22 acoustic measurements of the song of *P. m. mocinno* (red dots) and *P. m. costaricensis* (green dots), plotted as a function of latitude (total individuals is 21 *P. m. mocinno* and 15 *P. m. costaricensis*)

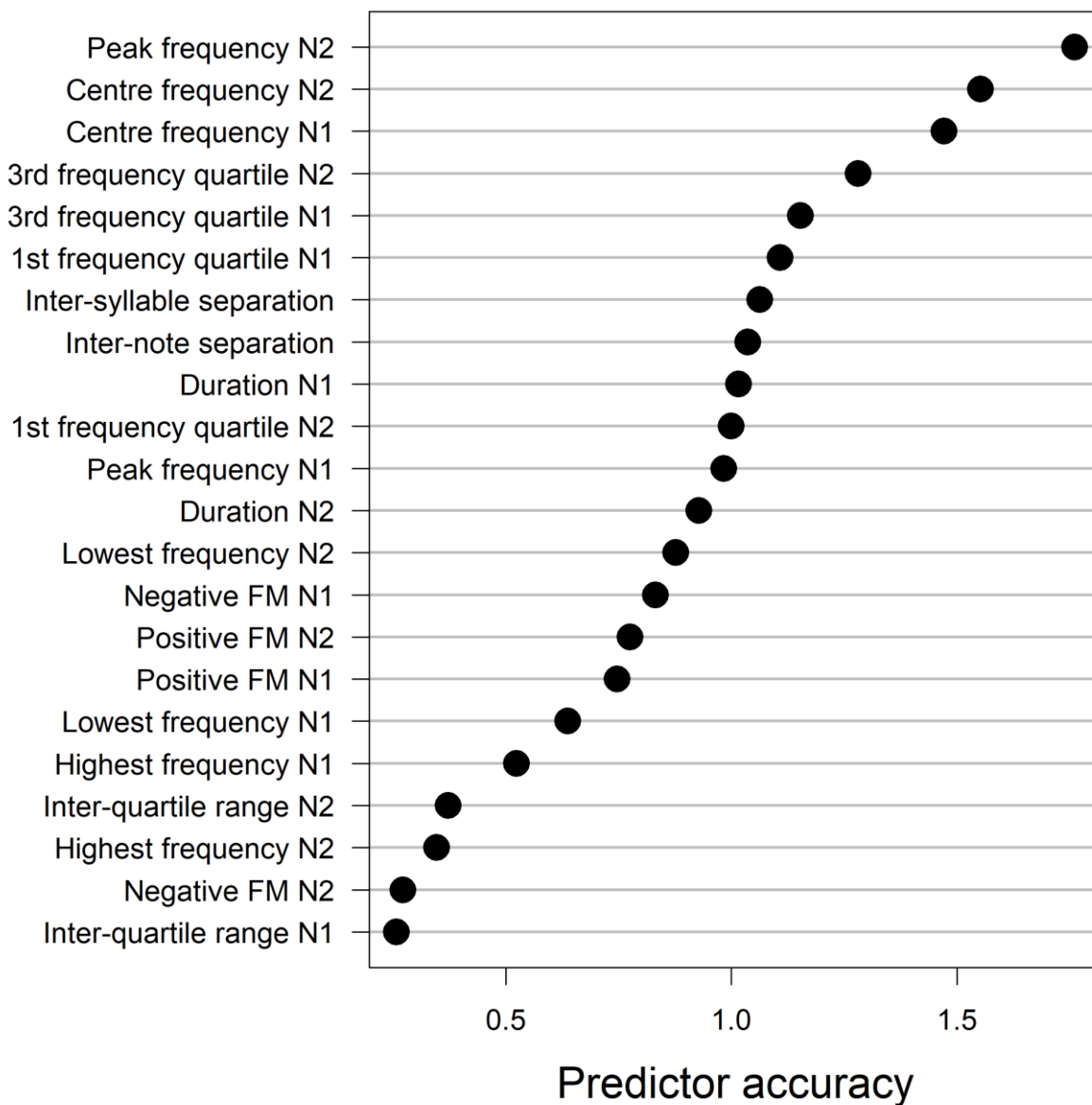


Figure 32: Random Forest analysis for *Pharomachrus* taxa. Relative importance of the explaining variables based on the mean decrease Gini impurity criteria

2.4.1 Molecular analyses

The divergence statistics in the 255 bp fragment of the Control Region between *P. m. mocinno* and *P. m. costaricensis* were: Da: 0.02763, dxy: 0.03091, uncorrected sequence divergence: 3.1%.

2.5 Discussion

Based on multivariate acoustic analysis and machine learning techniques, we could highlight a significant acoustic difference between *P. m. mocinno* and *P. m. costaricensis*, which we argue can support the separation of these taxa into two species. Then, following Solórzano and Oyama (2009), we consider that the previously allopatric subspecies could be regarded as two valid biological species, namely *Pharomachrus mocinno* (De la Llave 1832) and *Pharomachrus costaricensis* (Cabanis 1869). This taxonomic decision is determinant for conservation issues, highlighting the need to consider the elevation of *P. mocinno* and *P. costaricensis* to a higher global status of threat, which is fundamental to redirect conservation efforts on these rare and flagship species.

2.5.1 Song diversity among *Pharomachrus* species

The acoustic analysis showed a relatively important diversity among the *Pharomachrus* species, suggesting that each taxa bears a species signature in its song, a phenomenon commonly observed in birds but also in other singing species (Obrist et al. 2010). In particular, we found a difference in the acoustic parameters of *P. mocinno* and *P. costaricensis*, similar as it has been reported for other learning and non-learning species where species status has been promoted (Cadena and Cuervo 2010; Millsap et al. 2011; Sandoval et al. 2014, 2017). The correct classification between the two taxa was higher than the classification expected by chance as revealed by the LDA classification and confirmed by the RF classification among all *Pharomachrus* taxa. As non-passerine birds, species of *Pharomachrus* are supposed not to learn their vocalizations, so such differences between species of the family probably arise from genetic drifts, acoustic adaptation to environments, or sexual selection cumulated by years of separation.

In numerous species, body size is negatively correlated to sound frequency, a larger animal producing lower frequencies (Fletcher 2004; Martin et al. 2011). Here the peak, median, lowest and highest frequencies of the territorial vocalization of males of *P. mocinno* were higher than in *P. costaricensis*, when the first is significantly larger and heavier than the second (Solórzano and Oyama 2009). Such discrepancy between acoustics and morphology among-taxa has been observed for other bird species (Laiolo and Rolando 2003) and might suggest the occurrence of physiological or environmental evolutionary constraints. The morphological difference existing between the two species could be the consequence of different sexual selective pressures within the populations of *P. mocinno* and of *P. costaricensis*. It may also indicate that following a potential founder group, with representation of larger males, this characteristic are maintained by a sexual

selection process (Solórzano 2003). Moreover, plotting the discriminant function scores with respect to latitude did not reveal trends that would suggest clinal variation due to intergradation.

2.5.2 Integrative taxonomy of the Resplendent Quetzal and implications for conservation

A strong and discrete molecular differentiation was found between the two former *P. mocinno* taxa (Solórzano et al. 2004; Solórzano and Oyama 2009), implying that there is no female mediated gene flow between the two subspecies. We reanalysed the mtDNA data set of Solórzano *et al.* (2004) to have the same descriptive statistics of genetic divergence with those described between closely related species in other lineages. The divergence we found between the two taxa (3.1%) is similar to that described between other bird sister-species (Frankham et al. 2010), and in particular within the Trogonidae (1-4% in ND2 for sister-species in the Neotropical genus *Trogon* (DaCosta and Klicka 2008), 10-13% in ND2 for sister-species in the Asian genus *Harpactes* (Hosner et al. 2010)). The International Ornithological Committee (IOC) taxonomy (Gill and Donsker 2017) for the genus *Trogon* was based on the results from DaCosta and Klicka (2008) and resulted in the elevation of several subspecies to species status (*e.g.* *T. mesurus*, *T. ramoniamus*). Yet, these taxonomic changes were only made for 'traditional species' that were not monophyletic in the phylogenetic hypothesis proposed by DaCosta and Klicka (2008). Monophyletic species (*e.g.* *T. personatus*, *T. rufus*) with strong genetic differentiation (8%) across their distribution were not split (Gill and Donsker 2017). The genetic differentiation between the two *P. mocinno* subspecies is 3.1% for the analysed 255 bp of the Control Region fragment which usually has a comparatively higher substitution rate than protein coding genes in birds (Lerner et al. 2011). Furthermore, it could be difficult to representatively estimate the genetic divergence from such a short fragment. From a phylogenetic perspective, the two subspecies are reciprocally monophyletic and diverge from each other by a level of genetic divergence that is the low end of the range of genetic divergence between undisputed species. Hence, to give a more accurate estimate of the biological status of these taxa, the analyses of characters linked to the evolution of reproductive isolation (biometrics, vocalizations) were necessary.

For ethical reasons, due to the fact that *P. mocinno* and of *P. costaricensis* are rare, endangered and highly protected in Guatemala, it was unfortunately not possible to conduct playback experiments to test whether the individuals perceive the differences revealed by the analysis as usually achieved in behavioural experiments (Freeman and Montgomery 2017). Nevertheless, previous playback experiments showed that males of

P. mocinno could respond to territorial vocalizations of *P. costaricensis* (Solórzano and Oyama 2009) as actually did other species of the family Trogonidae responding to the same vocalizations tested (2007 personal communication from S. Solorzano to PB, unreferenced). This male failure to discriminate an allospecific song has been reported in other bird species (Nelson 1998; Soha et al. 2016) and does not preclude that females could discriminate allospecific territorial and courtship vocalizations in a mate choice context (Seddon and Tobias 2007).

The obvious acoustic differences between *P. mocinno* and *P. costaricensis* are in agreement with the morphology differentiation (LaBastille et al. 1972; Schulz and Eisermann 2017; Solórzano and Oyama 2009), the genetic differentiation (*i.e.* lack of shared haplotype implying no female mediated gene flow; (Solórzano and Oyama 2009) and the absence of contact due to an important geographical and climatic barrier (Powell and Bjork 1995).

The taxonomic decision to elevate *P. mocinno* and *P. costaricensis* at the species level has strong consequences for conservation. Traditional subspecies nomenclature can provide a misleading impression of the true geographical pattern of intraspecific differentiation and can arguably misdirect conservation effort (Zink 2004). At a global level, the former *P. m. mocinno* was classified as a Near Threatened species (Birdlife International 2016). Considering *P. mocinno* and *P. costaricensis* as species instead of subspecies leads to a significant reduction of the area of occurrence and also a reduction in the number of individuals for the populations of each species; thus the conservation status must be reconsidered to a higher level of danger. Moreover, both *P. mocinno* and *P. costaricensis* are vulnerable due to widespread deforestation, but the rate of habitat degradation being higher for the former than for the later (Sofia Solórzano et al. 2003), the modification of the conservation status could be higher for *P. mocinno*.

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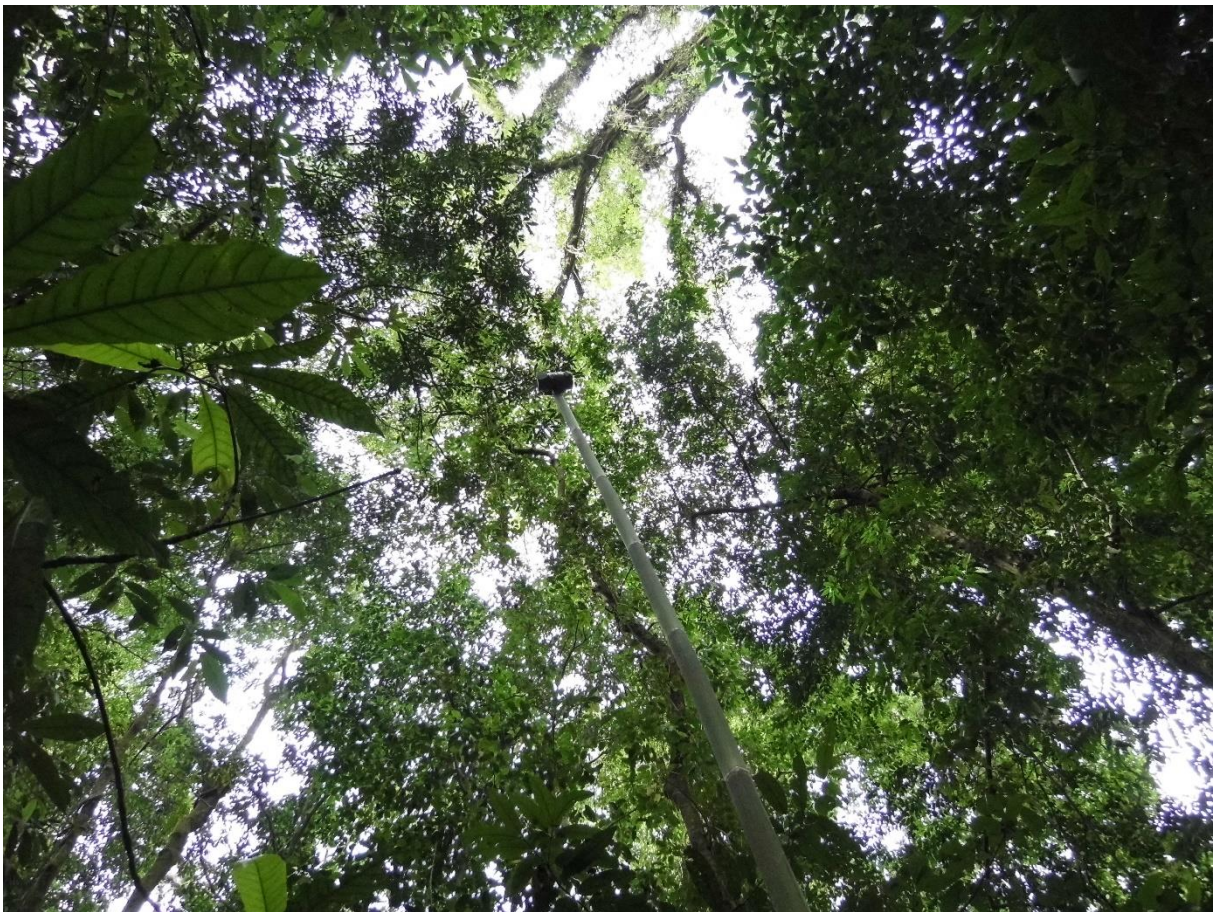
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Chapter 3: Automatic acoustic monitoring of the Resplendent Quetzal *Pharomachrus mocinno*



Speaker at the top of a bamboo rod intended to play P. mocinno recordings for propagation experiments in the cloud forest (Picture: Pablo Bolaños)

3.1 Summary

3.1.1 Context

The actual status of *P. mocinno* populations is not well documented, but the number of individuals is supposed to be decreasing. Conservation actions proposed for *P. mocinno* include monitoring population trends.

3.1.2 Problematics

The special characteristics of *P. mocinno* make it challenging to study. The observation of the species in the dense canopy is difficult and manipulation of individuals is controversial due to its high cultural importance. Then, we propose an acoustic methodology as a way to study the species in an effective and non-invasive way.

3.1.3 Methods

Recordings of *P. mocinno* were obtained by autonomous recorders. An acoustic automatic detection system was tested by a cross-correlation method. The range of the system to detect *P. mocinno* vocalizations (active range) was determined by sound propagation experiments. In addition, the impact of weather conditions on the number of detections was quantified by mixed model analysis.

3.1.4 Main results

The acoustic automatic detection system was efficient (85% of true positive detections). The range of the system to automatically detect *P. mocinno* vocalizations was determined. The number of detections was lower in 2016 (252000) than in 2017 (409451). The number of automatic detections was lower when the wind incidence was direct and when cloudiness was low.

3.1.5 Perspectives

The acoustic method can be applied to other areas and has the potential to become a warning system of perturbations or changes in *P. mocinno* populations due to human activities, including climate change.

3.1.6 Related communications and publications

Acoustic monitoring of *Pharomachrus mocinno*, a flagship bird species of Guatemala. Bolaños P., Sueur, J., Aubin, T. 2016. Oral presentation at the “Journées des Jeunes Chercheurs”, Paris.

Acoustic monitoring of Resplendent Quetzal *Pharomachrus mocinno*, a flagship bird species of Guatemala. Bolaños, P., Aubin, T., Sueur, J. Oral presentation at the European Conference of Tropical Ecology, 2017. Paris.

Acoustic monitoring of *Pharomachrus mocinno*, Resplendent Quetzal, a flagship bird species of Guatemala. Bolaños, P., Sueur, J., Aubin, T. Poster presentation at the African Bioacoustics Community Conference, 2018. Cape Town.

3.2 Introduction

The actual status of *P. mocinno* populations is not well documented, but the number of individuals is decreasing, mostly due to widespread deforestation (Birdlife International, 2016), but also caused by direct trapping and poaching, as well as trading of individuals and their upper-tail cover feathers (LaBastille & Allen, 1969).

Conservation actions proposed for *P. mocinno* include monitoring population trends (Collar, 2001). The species has been studied by methods like point counts or line transects (Yurrita, 2013; Avila et al, 1996). Other studies have used telemetry to track the movements of individuals (Yurrita, 2013; Paiz, 1996; Powell & Bjork, 1995). Such studies have been of great value and highly contributed to the knowledge of the species. Nevertheless the survey of the species is challenging due to its elusive behaviour and the density of the canopy in the cloud forest, which complicates its observation. The feathers of *P. mocinno* can easily be mistaken with the green background of the forest (Monge-Najera & Hernandez, 1994). Furthermore, human presence in the field can change their behaviour, which can result in a source of bias. Monitoring techniques like point counts usually are limited to short sampling periods, for instance 5 to 10 min (Ralph et al, 1997), which could be not enough to register activity of cryptic species. Moreover, disturbing *P. mocinno* individuals being considered a non-ethical practice in Guatemala, invasive methods requiring individual manipulation could be not recommended. Devices installation for telemetry or GPS tracking require manipulation of individuals and uninstallation of devices can be highly difficult, requiring catching the same individual a second time which is generally not accomplished. In consequence, devices can remain installed on individuals several years after the study ends (*personal observation*). These transmitters can increment mortality by predation or accident or can decrease reproduction

success (Mech & Barber, 2002). Thus, a proper analysis of benefits and costs is necessary to consider before conducting studies including such methodologies.

Another method with great possibilities to study the Resplendent Quetzal is to record and analyse their vocalizations. Acoustic survey methods are non-invasive and does not require human presence. Decades ago, it has been suggested the need to sophisticate census techniques using recordings of territorial vocalizations of male Resplendent Quetzal (LaBastille & Allen, 1969) but until now it has never been developed nor tested.

Acoustic monitoring has been conducted on several bird species with success. Acoustic methods for estimating species richness has been found to be a suitable alternative to point counts (Haselmayer & Quinn, 2000). For example, acoustics has been used to estimate population density of Ovenbirds (*Seiurus aurocapilla*) (Dawson & Efford, 2009) and Corncrakes (*Crex crex*) (Peake & McGregor, 2001). The use of recording devices is ideal to study cryptic species, difficult to observe, and has resulted a highly less expensive method than studies based on field observers (Williams et al, 2018).

The increasing availability of automatic recorders has made possible to sample several sites at the same time, with specific configurations and time schedule (Knight et al, 2017a). Autonomous recording can be useful in areas where visibility of individuals is limited, or when the species behaviour or morphological characters make them difficult to observe (Williams et al, 2018). Identification of species by recordings has given similar detection results compared to point counts, when studying the riparian corridors of southern California (Celis-Murillo et al, 2009).

As a result of the continuously increasing use of autonomous recorders for bird monitoring, the quantity of recordings has reached enormous amounts. Therefore, the accumulation of recording data rapidly became difficult to analyse using manual methods and can be a high time consuming task. Thus, automatic sound recognition protocols started to be necessary and has attracted the attention of the scientific community. Automatic detection methods bring the possibility to quantify error rates, which is too difficult or not possible to control with manual methods based on human observers (Katz et al, 2016a). In bird monitoring programs, the association of point count methods with automated acoustic detection has been recommended, both methods having strengths and weaknesses (Leach et al, 2016). Automatic detection methods appears as an extremely efficient alternative to human based point counts (Digby et al, 2013). For example, automated signal detection has been effective to study the presence-absence and call rate of a nocturnal species (Knight et al, 2017b). It has also been used with success for the study of species with cryptic behaviours (Goh, 2011).

Automated acoustic monitoring could save costs and solve problems of unavailability of experts in the field. In addition, automatic detection can be used to analyze faster and with a known error rate large datasets. Furthermore, avoiding the human presence in the habitat surveyed may decrease or eliminate the bias caused by changes in behavior of the species surveyed. These characteristics could be substantial in monitoring programs of species difficult to observe or manipulate due to cultural relevance as *P. mocinno*.

The objective of this study was to develop an automatic acoustic detection system, using autonomous recorders, to follow the vocal behaviour of *P. mocinno* and to track in space and time populations. To achieve that, recordings were taken in a cloud forest in Guatemala by autonomous recorders during 15 days in the beginning of the breeding season during two consecutive years.

Automatic detections were based on the principle of cross-correlation between a template of a target species vocalization and recordings of a survey. Propagation experiments were also conducted to determine the working range (active space) of the detection system. At last, an analysis of the potential influence of meteorological conditions on acoustic detections was conducted to explain eventual differences found by year.

The results obtained suggest that the acoustic automatic detection system developed is efficient and gives interesting information about the presence and activity of *P. mocinno*. The range of the automatic recognition system has also been determined, and this information can be applied in sampling protocols of future studies. The results showed that the number of automatic detections is not independent of some environmental factors. The acoustic method of detection described here can be adapted to apply in other areas and has the potential to become a warning system of perturbations or changes in *P. mocinno* populations due to human activities or climate change.

3.3 Materials and Methods

3.3.1 Study area

Field work was conducted at “Los Andes”, Suchitepéquez (14° 32' - 91° 11', 1992 m). “Los Andes” is a private reserve including 607 ha on the southern slope of the Atitlan volcano at an elevation of 840 – 1830 m.a.s.l., with a cloud forest on the higher part of the reserve (364 ha) and crops of coffee, tea and rubber on the lower part (243 ha) (Figure 33) (Familia Hazard et al, 2004).

It has been reported 218 bird species in Los Andes, which is part of the Guatemalan volcanic chain, considered a high endemism area. Important endemic species of the volcanic chain in Mesoamerica occurring in Los Andes reserve are, the Horned Guan (*Oreophasis derbianus*), Cabanis Tanager (*Tangara cabanisi*), Bearded Screech-owl (*Megascops barbarous*), and the Resplendent Quetzal (*P. mocinno*), among others (Familia Hazard et al, 2004).

Recordings were taken in an area with cloud forest, with typical vegetation including some important tree species for the Resplendent Quetzal like, aguacatillo (*Ocotea dendrodaphne*) and amate (*Ficus* sp.). The undergrowth includes species like pacaya (*Chamaedorea elegans*) and arborescent trees (*Cyathea* sp.).

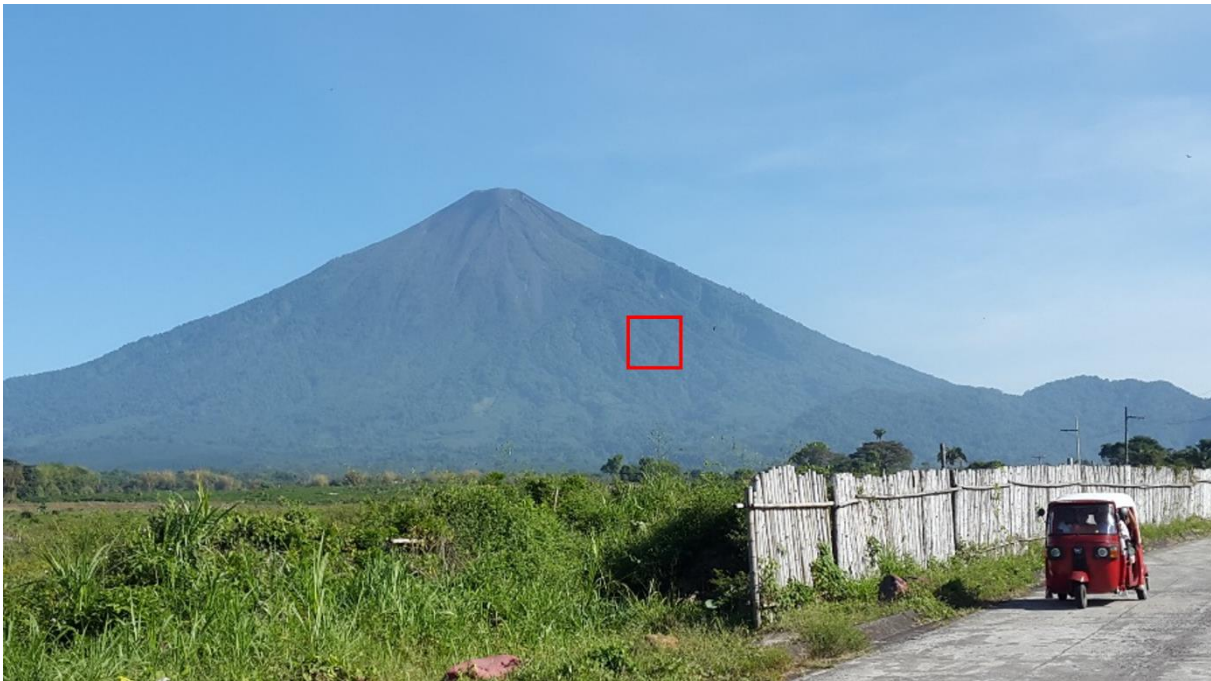


Figure 33: Study site (red square) at Los Andes private reserve, located in the southern slope of the Atitlan volcano

3.3.2 Automatic detection

The soundscape of the forest was simultaneously recorded by SM2 automatic recorders (Wildlife Acoustics®) distributed on four sites, with an average separation of 450 m between each recorder (Figure 34) (14.550658° -91.181145° , 14.547825° -91.178696° , 14.545896° -91.185870° , 14.584563° -91.181422°). Recorders were deployed during 15 days in February (10th to 24th) 2016, 6 days in January (26th to 31th) 2017 and 9 days in February (6th to 12th and 24th to 25th) 2017. The soundscapes were recorded at a sampling frequency of 44.1 kHz and a depth of 16 bits. Recorders were

configured to record with a gain of 12 dB. This generated a total of 1440 recordings of 30 minutes.

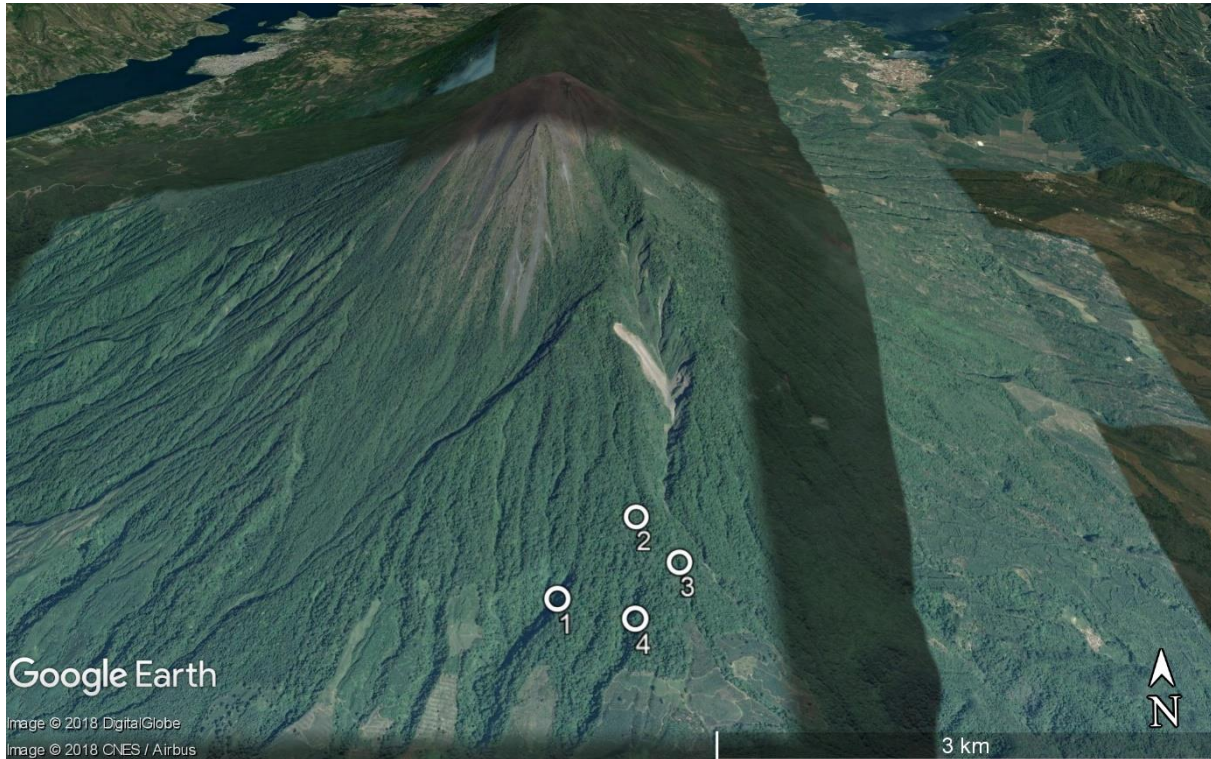


Figure 34: Location of the four automatic recorders at Los Andes private reserve, working 15 days in 2016 and 15 days in 2017

3.3.2.1 Evaluation dataset

A dataset consisting of 44 recordings of 10 min randomly selected among the 1440 recordings of 30 min was created to train and test the acoustic detection system. Among the four vocalization types of *P. mocinno*, the territorial vocalization was the most frequent in recordings. It consists of syllables composed by two notes with one note higher in frequency than the other. The territorial vocalization is the most stereotyped, simple and repetitive among the vocalizations of *P. mocinno*. It was selected among the other vocalizations to automatically detect the presence of *P. mocinno* because territorial vocalizations are known to encode species-specific information (Stoddard, 1996) and because template matching detection methods, like cross-correlation, work well with stereotyped vocalizations (Stowell 2017).

A total of 2642 notes of the territorial vocalizations coming from 44 recordings of the dataset were manually selected and analysed with Raven Pro 1.4 software (www.birds.cornell.edu/raven) with a time precision of 0.0232 s measured on the oscillograms, and a frequency precision of 21.5 Hz measured on the spectrograms. The

parameters for each note, beginning and ending times, and the lowest and highest frequencies, were manually selected. These notes were used to test the automatic detection system.

3.3.2.2 Template creation

To evaluate the presence of *P. mocinno* vocalizations, one template from each recording site was created, resulting in a set of four templates. Only good quality sounds with a high signal to noise ratio were chosen. Templates intended for detection by cross-correlation were created with the R (Development Core Team, 2008) package `monitoR` (Hafner & Katz, 2015), using a 512 point FFT window length with no overlap, a Hanning window function and a bandwidth from 0.5 to 2 kHz (Figure 35). The correlation template was based on a matrix of amplitudes, and the values for amplitudes were copied from the template spectrogram (Katz et al, 2016b).

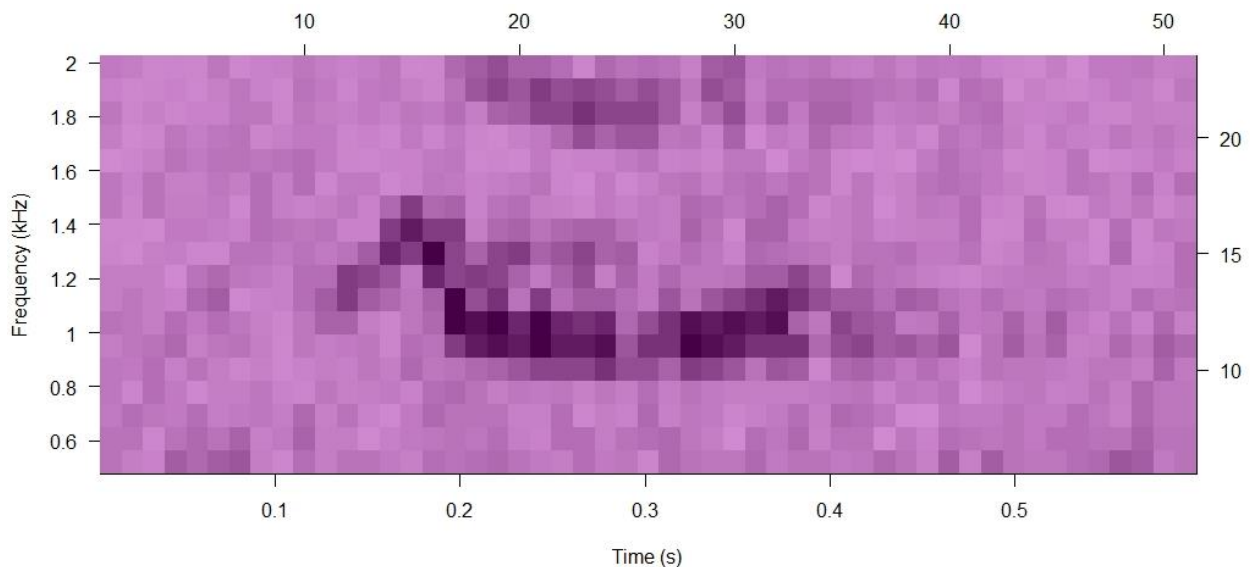


Figure 35: Template of a territorial vocalization for cross-correlation detection. Four different templates were used, one for each recording site

3.3.2.3 Detection rates

The recordings of the evaluation dataset were analysed by cross-correlation with the four templates. Sliding spectrograms with the same characteristics as the templates were applied throughout the recordings of the evaluation dataset. The cross-correlation gives a score for each frame based on the Pearson correlation coefficient (Mellinger and Clark, 1997) (Figure 36). A table with different correlation score peaks resulted from the process of correlation. To avoid duplicate selections, as multiple templates were used, a condensation of the peaks obtained were made by selecting the higher score within a time

tolerance of 2/3 of the duration average of the four templates created, as recommended by Hafner & Katz (2015).

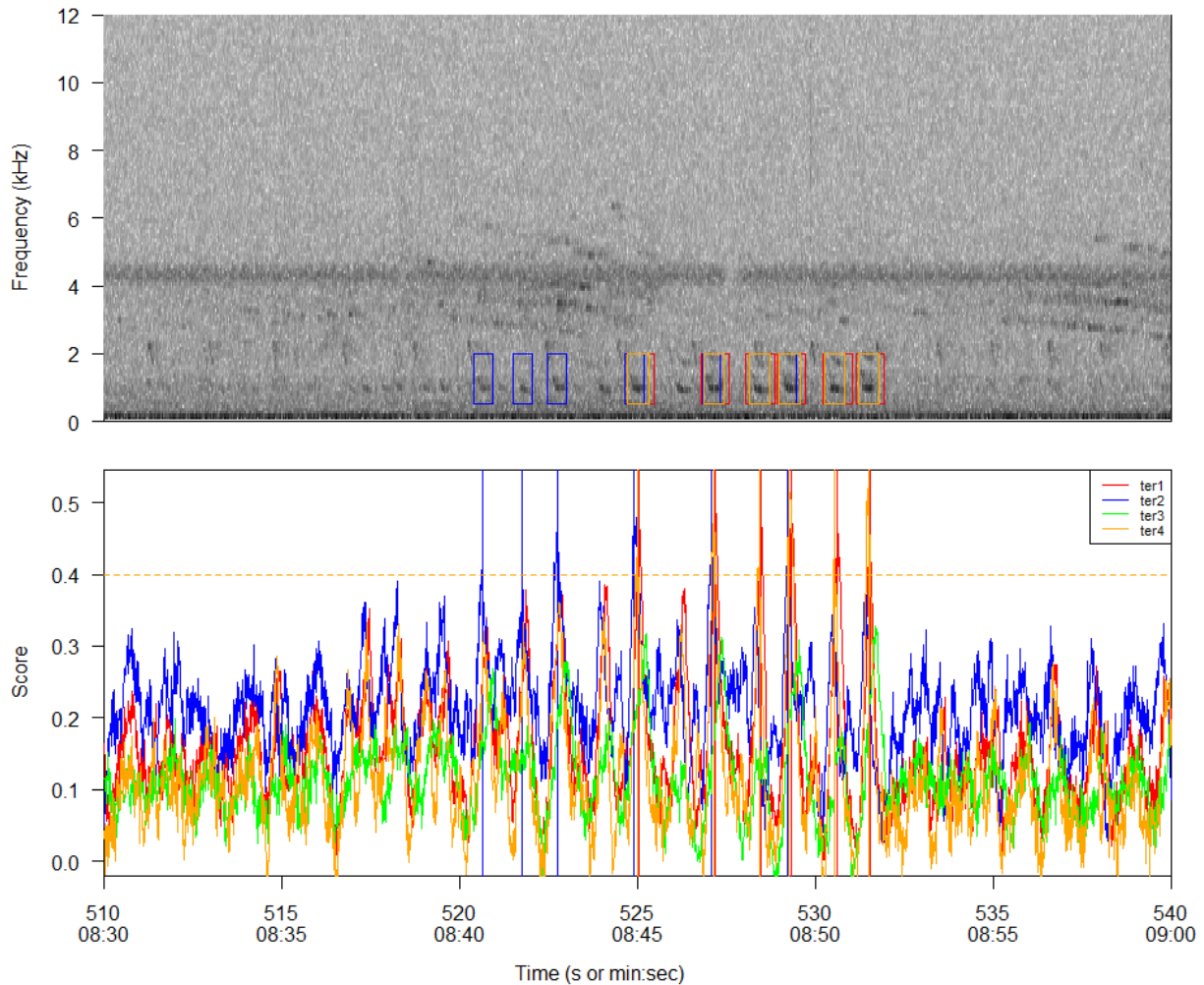


Figure 36: Cross-correlation process. Bottom: The different coloured lines represent the evolution of the correlation scores of different templates (one colour per template). The threshold score cut-off was established at 0.4. Scores obtained above this threshold value were classified as true detections. When two or more templates detected a vocalization at the same time, the highest score was chosen in a post hoc process. Top: spectrographic view with detections highlighted with coloured frames

Detection rates depending on the score cut-off used were obtained by a comparison of the manual selections and the detections obtained by the cross-correlation, using different score cut-off (θ) values between 0 and 1. Detections were identified as true positives (TP) when the detection co-occurred in time with a manual selection and scores above or equal to the score cut-off. A detection that scores below the score cut-off was classified as false negative (FN). False negative detections resulted of a manual selection failing to co-occur with any automatic detection. True negative (TN) detections are a

product of an automatic detection does not co-occurring with any manual selection, and false positive (FP) detections are automatic detections failing to co-occur with a manual selection, and scoring above or equal to the score cut-off (Figure 37).

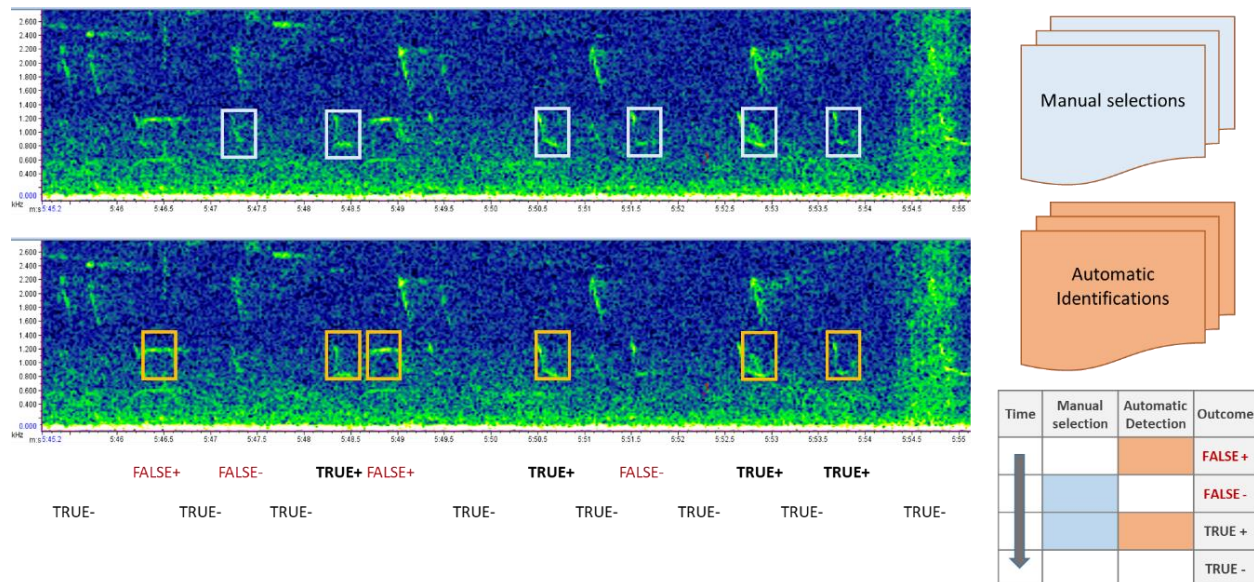


Figure 37: Evaluation of automatic detections compared to manual selections. Manual annotations (top) are compared to automatic detections obtained through cross-correlation (bottom) so that the automatic detection is considered either as true positive (TP), a true negative (TN), a false positive (FP) or a false negative (FN) as shown in the inset table

In order to classify the automatic detections, as TP, TN, FN or FP, a time tolerance was selected to consider if a detection and a manual selection co-occurred through a specific time period. The time tolerance for this process was chosen after doing a comparison of the area under the curve (AUC) of the receiving operating characteristics (ROC) curve, obtained by combinations of different score cut-offs between 0 to 1 and different time tolerances between 0 and 2 s (Figure 38). Thus, the time tolerance chosen to evaluate the system (0.5 s) was the one that gives the highest AUC (0.86) of the ROC curve.

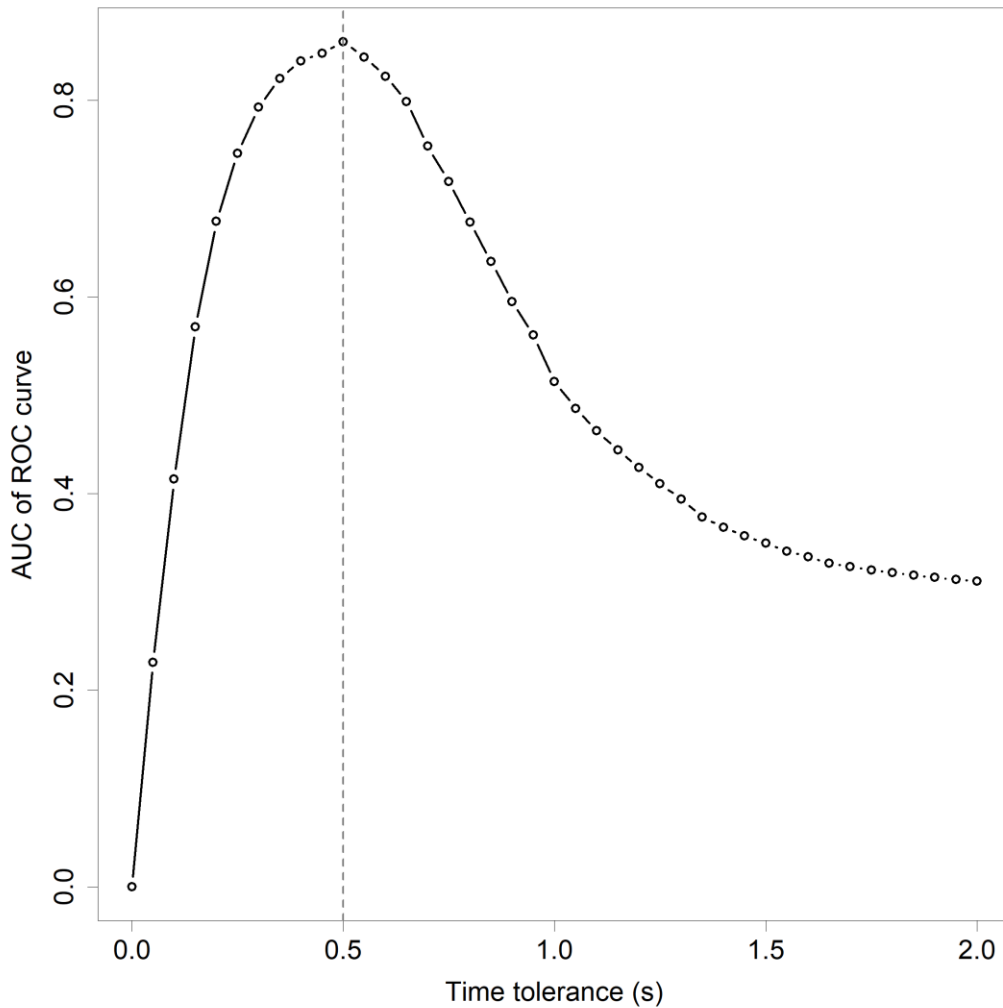


Figure 38: Area under the curve (AUC) of the receiving operating characteristics (ROC) curve obtained by combinations of different score cut-offs (θ) between 0 and 1 at different time tolerances (between 0 and 2) for the evaluation of the detection rates by cross correlation. The higher AUC was obtained at a time tolerance of 0.5

Detection rates at variable score cut-offs between 0 and 1 were determined in order to choose the best score cut-off according the objectives of the research (Figure 39). Finally, a score cut-off of 0.4 was chosen, giving more importance to the specificity (high TN rate) rather than to the sensitivity (high TP rate), a choice that is most commonly suitable for conservation purposes. Calculation of detection rates is summarized in the following equations:

$$\text{TP rate} = \sum \text{TP} / \sum (\text{TP} + \text{FN})$$

$$\text{FP rate} = \sum \text{FP} / \sum (\text{TN} + \text{FP})$$

$$\text{TN rate} = \sum \text{TN} / \sum (\text{TN} + \text{FP})$$

$$\text{FP rate} = \sum \text{FN} / \sum (\text{TP} + \text{FN})$$

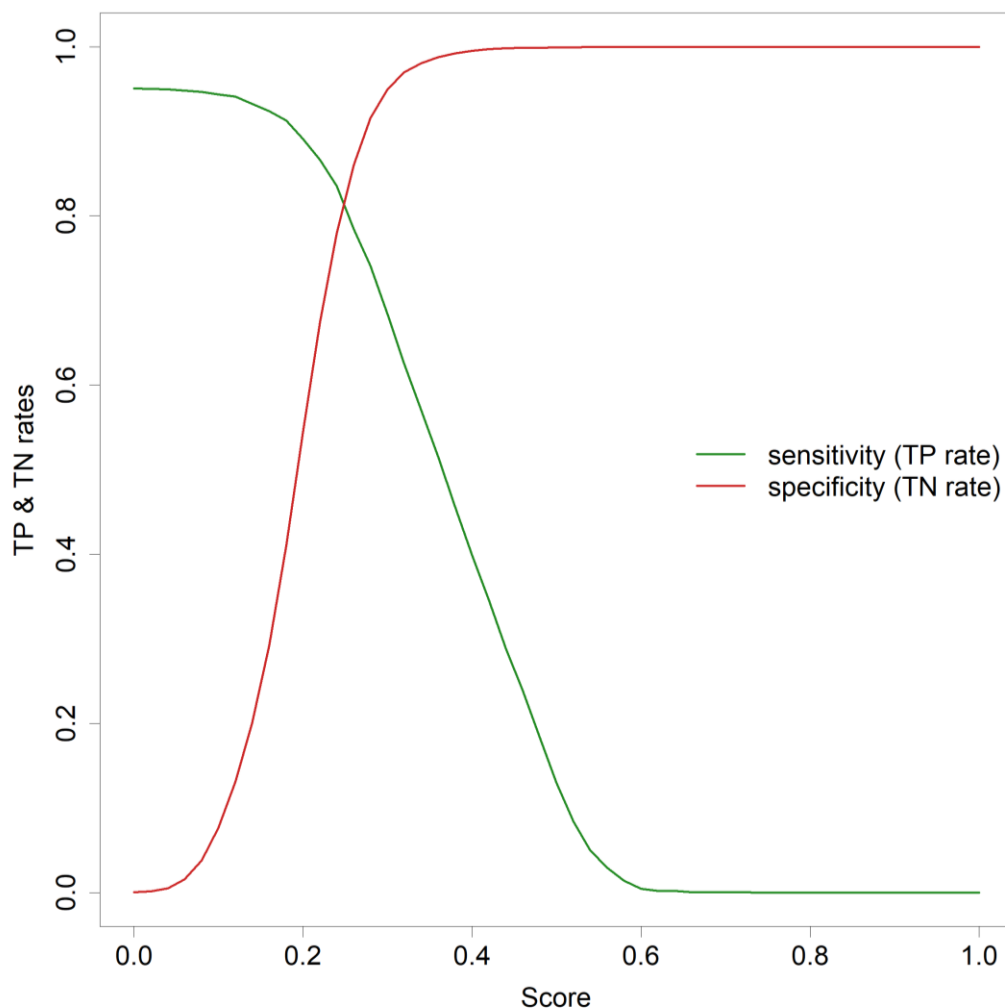


Figure 39: Sensitivity (green line) and specificity (red line) for detection by cross-correlation at varying score cut-offs (θ) between 0 and 1

3.3.3 Detection working range

In order to determine the working range of the automatic recorders used, sound propagation experiments were carried out at “Los Andes”. Territorial vocalizations of *P. m. mocinno* were synthesized on the basis of representative natural vocalizations previously recorded. Synthetic vocalizations were built using the graphic synthesizer of the Avisoft SASLabPro software version 4.15 (Avisoft Bioacoustics, R. Specht–version 3.74) that extracts the frequency contour of the fundamental frequency, the relative amplitude of the different harmonics and the amplitude envelope of the natural vocalization. This procedure ensured to use sounds that do not contain any background

noise and any propagation effect due to the recording of vocalizations in the habitat. One synthetic territorial vocalization was built and edited in a single sound file with 15 repetitions, with a silence of the same length of each vocalization type between each repetition.

The series of synthetic sounds was played back by a loudspeaker FoxPro Fury 2 with a mean sound pressure level corresponding to the estimated natural level of the calls emitted by the species (80 dB_{SPL} measured at a distance of 1m from the loudspeaker). The propagated sounds were recorded at a sampling frequency of 44.1 kHz and a 16 bit dynamic range, with a Wildlife Acoustics SM2 automatic recorder. The SM2 recorder was fixed at a starting central point (N 14°32.678'; W 91°11.145') corresponding to the typical habitat of *P. mocinno*. To evaluate the active recording space of the SM2, the loudspeaker was moved away from the starting point to record at six distances, 1 m (control), 4, 8, 16, 32, 64 and 128 m, at each transect (front, right, back and left directions). The SM2 recorder was placed at a height of 1.7 m corresponding to the height at which the other SM2 recorders could be easily installed, and the loudspeaker was placed at a height of 7 m corresponding to the usual calling height of *P. m. mocinno*. The geographical coordinates of each playback were taken with a GPS Garmin 64S and the distances between the loudspeaker and the microphone were measured with a Laser meter Leica Disto D8. The ambient temperature and the relative humidity were measured with a Multi Sensor Ermes 01. To evaluate the attenuation of the propagated signals, six sound pressure levels in dB were measured with a sound level meter Testo 815 (fast setting, A scale, 50-100 dB range) at each distance during the playback and averaged.

To quantify the degradation of the vocalizations during propagation, for each distance, the spectrograms of the propagated signals were cross-correlated with the control signal (1m) using 0.1, 0.2, 0.3 and 0.4 score cut-offs. The analyses were run with the R package `monitor`.

3.3.4 Fluctuation of vocal activity in relation with environmental factors

The cross-correlation template matching was applied in the recordings obtained in 2016 and 2017, using the same parameters described above. The detections obtained were summed by hour. To analyse the possible influence of environmental factors on the number of detections, data from the closer meteorological station of the INSIVUMEH (“Instituto de Sismología, Vulcanología, Meteorología e Hidrología”), “Estación Meteorológica de Santiago Atitlán”, were recorded by day. The meteorological data taken in consideration were: average wind direction (°), average cloudiness (*oktas*), average rain (mm), average wind velocity (km/h), average relative humidity (%) and average

temperature ($^{\circ}\text{C}$). The wind direction was also analysed. The meteorological station is located at approximately six km away from the volcano measuring wind directionality as it comes from any side around the station. As the study site was located on the south slope of the volcano, wind strikes the site directly if it comes from the south, but if the wind comes from the north, the volcano works as a barrier, protecting the southern slope from the direct wind. Data of wind directionality were available with a resolution of 45° , with 0° corresponding to a direct incidence coming from the south, and 180° an opposite direction coming from the north, at the rear side of the study site. The other directions (90° and 135°) were merged as the same relative directional incidence of 90° if the wind came from the opposite left and right sides (Figure 40).

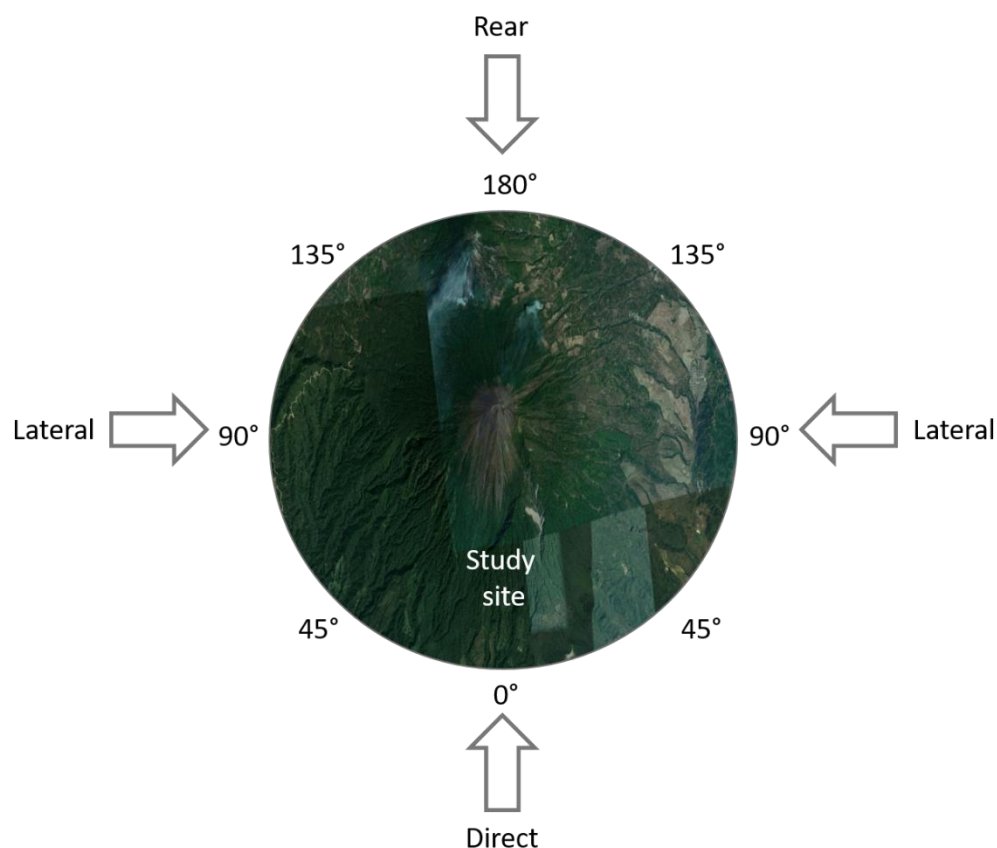


Figure 40: Direction incidence of wind in relation to the study site located in the southern slope of the Atitlan volcano

3.3.5 Statistics

To explain differences in the acoustic activity by year, a linear mixed effect analysis was built with the environmental variables as fixed effects, namely: average wind direction ($^{\circ}$), average cloudiness (*oktas*), average rain (mm), average wind velocity (km/h), average

relative humidity (%) and average temperature (°c) as fixed effects (without interaction term). Number of detections by hour was the response variable, and time of day and site were included as random effects. Number of detections were not log-transformed, because it is not recommended on count data (O'Hara & Kotze, 2010; Brooks et al, 2017). Mixed model analysis was performed with the R package glmmTMB (Magnusson et al, 2018) adapted to analyse count data, the package works increasing the range of models that can be fitted using maximum likelihood estimation (Brooks et al, 2017). Due to an over dispersion of data, a negative binomial distribution model was then conducted. Interaction between variables was tested by determination of Variance Inflation Factors (VIF, Field, 2009) for a standard linear model excluding effects and interactions, this was performed with the R package car (Fox, 2018). It revealed a VIF of 3 or less for all the environmental variables, values greater than 3 can lead to biased results in the regression (Zuur et al, 2007), thus all variables were kept in the analysis. Critical probabilities (p) values were obtained by likelihood ratio tests of the full model with the effects in question against the model without one of the effects at a time.

3.4 Results

3.4.1 Automatic detection

The algorithm was tested on 6.67 hours of recordings, with different classification thresholds to obtain the ROC curve and detection rates. The ROC curve had an area under the curve (AUC) of 0.86 (Figure 41). At a threshold cut-off of 0.4, the algorithm obtained a TP rate of 39.89 % and a FP rate of 0.45%.

The bird species triggering FP detections were, in decreasing order of occurrence: *Odontophorus guttatus*, *Herpetotheres cachinnans*, *Penelope purpurascens*, *Aulacorhynchus prasinus* and *Penelopina nigra*. There were also FP detections due to noise of planes, falling objects and other unknown sources (Figure 42).

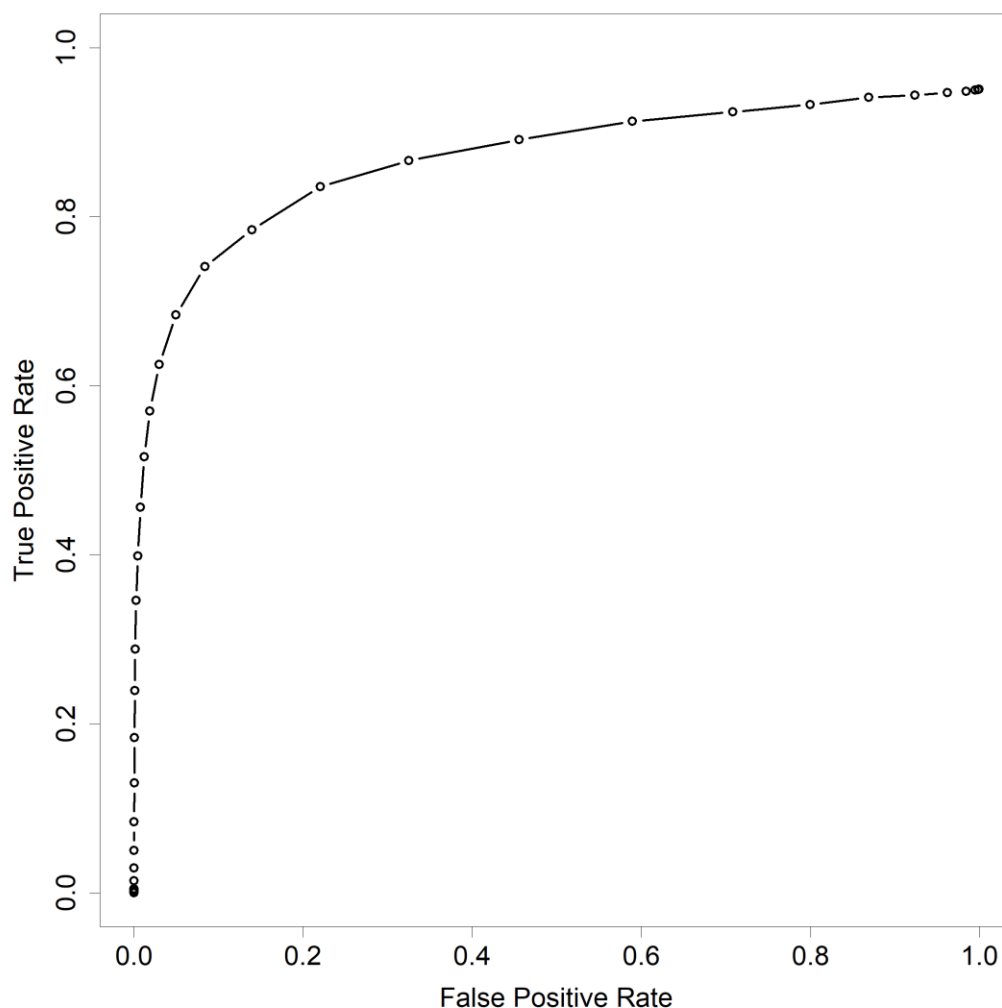


Figure 41 - Receiver Operating Characteristic (ROC) analysis for the detection of vocalizations of *P. mocinno* by cross correlation. The area under the curve (AUC) obtained is 0.86

3.4.2 Detection working range

The number of TP detections obtained for each distance with different score cut-offs is presented in Table 8. There was a negative relation between the score cut-off and the number of detections. For a score cut-off of 0.3, 97% of the vocalizations were detected until 64 m at the front of microphone, 93% on the left, 77% on the right, and 60% in the back. For a score cut-off of 0.4, the detections decreased strongly with distances, with an effective detection range of about 16 m (43% front, 50% left, 57% right, 27% back). At 64 m, with the same threshold of 0.4, the percentage of detection became null at back and left. Figure 43 shows the working range of the automatic detection system according to different score cut-offs.

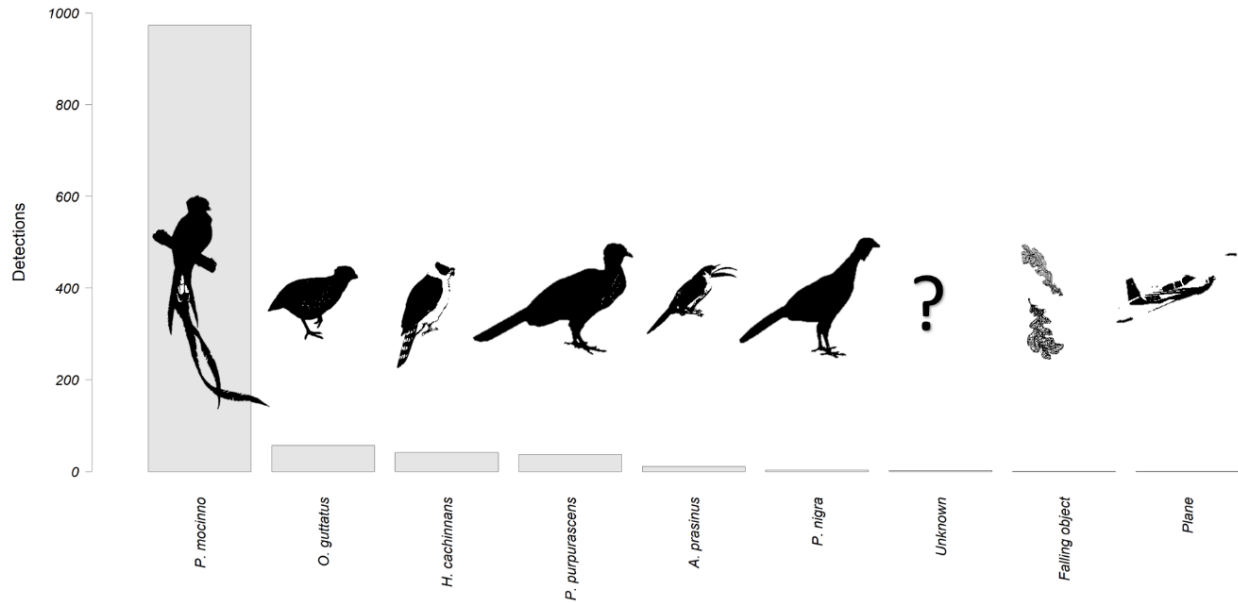


Figure 42: Vocal species and other noise sources triggering false positive detections of *P. mocinno* through cross-correlation

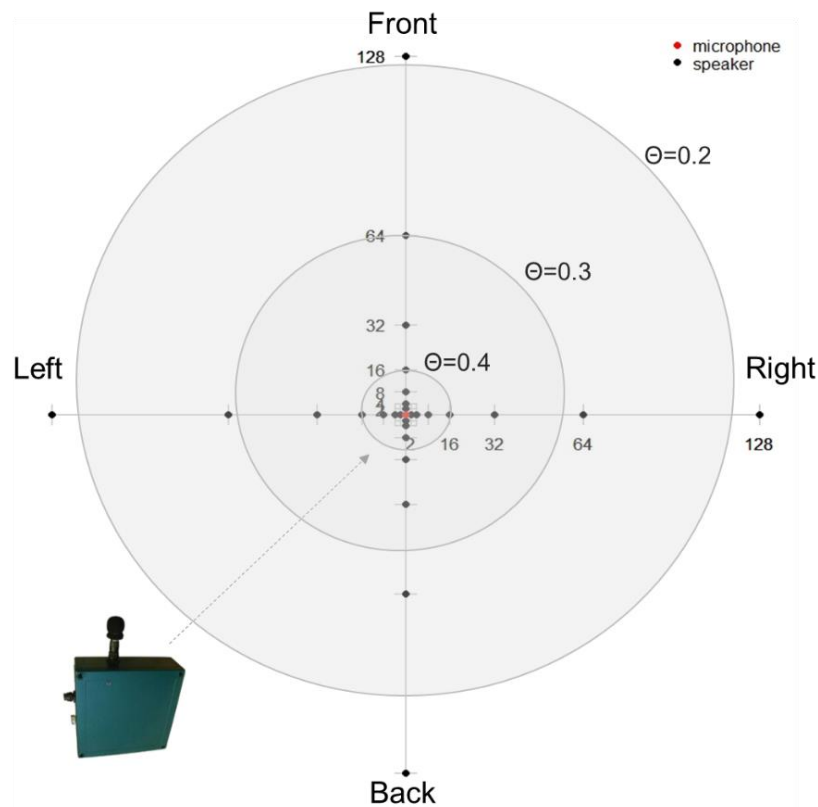


Figure 43: Working range (grey circles) of the detection of *P. mocinno* vocalizations by cross correlation at different distances according to three different score cut-offs

Table 8: Percentages of true detections of *P. mocinno* vocalizations by cross correlation, at different distances and Pearson score cut-offs (θ)

Direction	Distance (m)	cut-off: 0.1	cut-off: 0.2	cut-off: 0.3	cut-off: 0.4
Front	4	100	100	100	50
	8	100	100	100	50
	16	100	100	100	43
	32	100	100	97	0
	64	100	100	97	13
	128	97	90	30	0
Right	4	100	100	100	50
	8	100	100	100	53
	16	100	97	97	57
	32	100	100	97	23
	64	100	97	77	13
	128	97	87	43	0
Back	4	100	100	100	50
	8	100	100	100	43
	16	100	97	97	27
	32	100	100	90	0
	64	97	83	60	0
	128	93	27	0	0
Left	4	100	100	100	50
	8	100	100	100	43
	16	100	100	100	50
	32	100	97	97	0
	64	100	97	93	0
	128	97	73	3	0

3.4.3 Fluctuation of vocal activity in regard to environmental factors

A total of 661,451 detections were obtained for the 30 days (420 h) of the two years of acoustic survey. The number of detections in 2017 was higher than in 2016, with respectively 409,451 and 252,000 detections (Figure 44). Mixed model analysis revealed that there were more detections when the wind came from north, rear of the volcano in respect to the study site (Figure 45), wind velocity was also important with less detections when the velocity was higher.

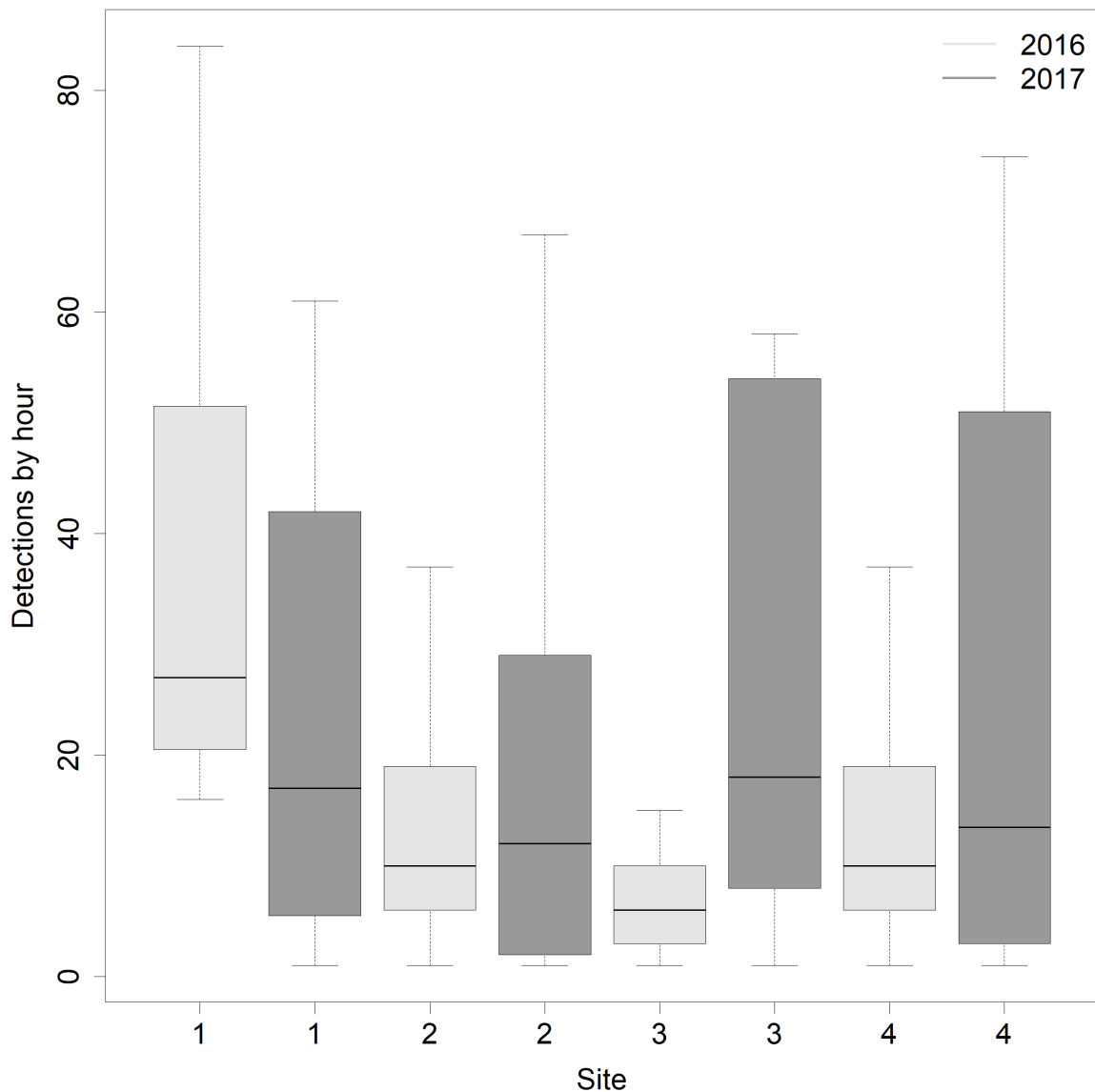


Figure 44: Number of detections of *P. mocinno* vocalizations by hour, in each site in 2016 and 2017

Cloudiness was the third most important environmental variable, with more detections when the cloudiness was higher (Figure 46). Wind direction affected detections ($X^2(1)=25.9830$, $p=3.445e-07$) decreasing them by about 0.0076 ± 0.0011 (standard errors). Wind velocity affected detections ($X^2(1)=8.9493$, $p=0.0028$) decreasing them 0.2039 ± 0.0665 (standard errors). Cloudiness affected detections ($X^2(1)=4.1523$, $p=0.0416$) increasing them by about 0.2743 ± 0.0665 (standard errors).

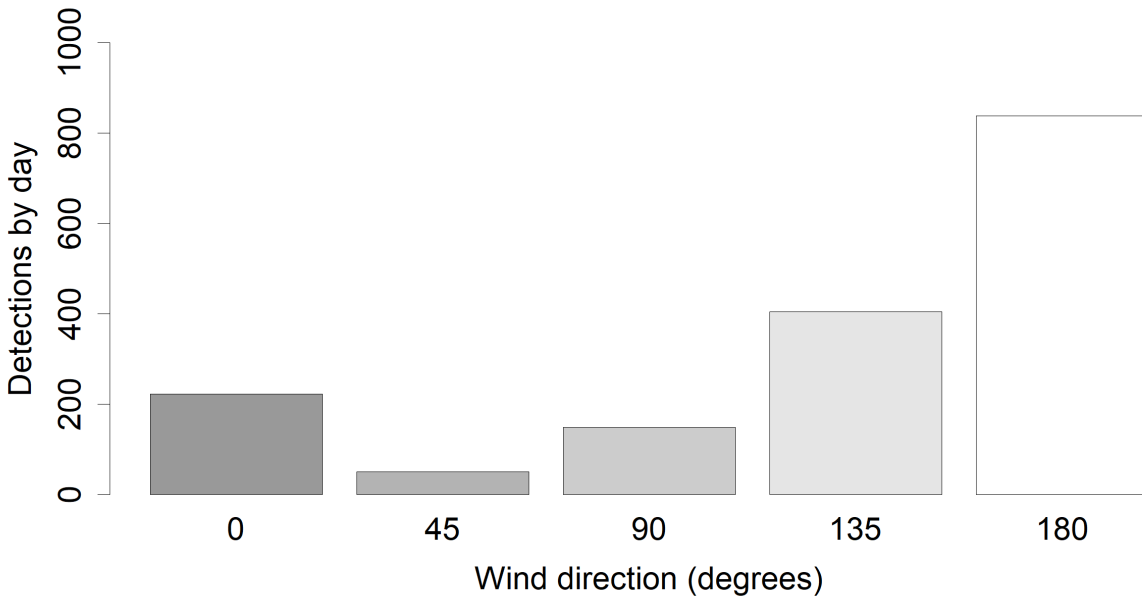


Figure 45: Number of detections of *P. mocinno* vocalizations by cross-correlation, according to the wind direction in relation to the study site (southern slope of Atitlan volcano). 0° corresponds to a direct incidence of the wind (coming in front of the slope of the study area) and at 180°, is indirect (coming from the rear side of the volcano). Values between 45° and 135° are lateral wind incidence

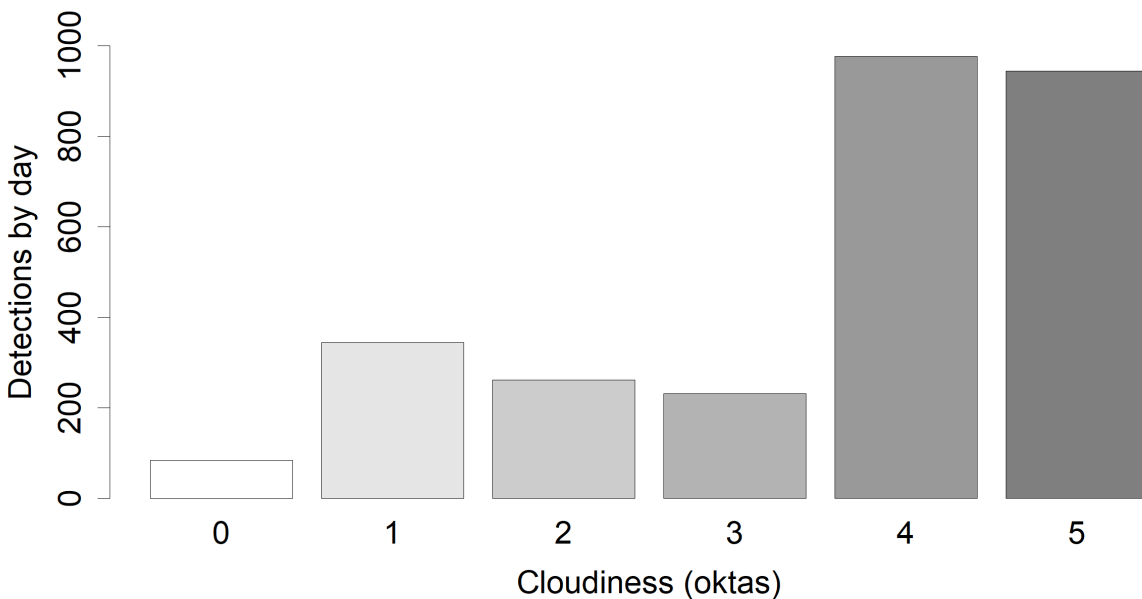


Figure 46: Number of detections of *P. mocinno* vocalizations by cross-correlation according to the cloudiness level

3.5 Discussion

An automatic system to detect the vocalizations of *P. mocinno* taken by autonomous recorders was developed and tested. The working range (active space of detection) of the automatic acoustic detection method was determined. In addition, a mixed model analysis was conducted in order to test the possible influence of weather on the number of detections.

The vocal activity of *P. mocinno* is highly unpredictable and rare, even during the breeding season. The behaviour of *P. mocinno* makes their direct observation challenging because individuals can often stay perched quiet in the canopy and can be cautious if they detect human presence. Thus, continuous survey with autonomous recording equipment appears as an ideal solution to increase the chance of detection of this cryptic species.

Although the detection system could be improved, the algorithm used, based on cross-correlation, was sufficiently efficient in analysing several recording hours and could be used to conduct monitoring programs of *P. mocinno*.

Among the automatic detections, the FP were mostly caused by other bird species and to a lesser extent by falling objects and planes. Nevertheless, the proportion of FP was low compared to the number of TP obtained. The identification of species causing FPs gives the possibility to improve the algorithm for future studies. This could be done, for example with the creation of templates to detect also the vocalizations of the most problematic species. This process could assign a correlation score higher for the templates of the problematic species than for the ones of *P. mocinno*. Then, a cleaning of the database could be done by the process of condensation described in the methodology, discarding the species belonging to these templates.

According to the sound propagation experiments, the working range of the autonomous recorders resulted in a circle of detection surrounding the microphones not completely symmetrical. Instead, the range of detection to the front is greater, less to the sides and even lower to the back direction. In addition, different score thresholds used in the automatic detection resulted in different ranges of detectability. This information will be highly useful to design the spatial configuration of the recorders. Furthermore the range information of detectability make possible to estimate the distance at which the species was recorded in a survey. This information could lead to a well-designed sampling protocol, taking in consideration the positioning of the recorders, could avoid over-counting occurring when recorders are positioned too close compared to their range of detection (pseudo-replication).

The number of detections was higher in the second year of recording (2007) than in the first one (2006). Multifactorial analysis revealed that wind direction incidence and cloudiness were the more important features which influences the acoustic activity detected by year. Direct wind direction incidence had a negative impact, decreasing the number of detections. Probably, the acoustic activity of *P. mocinno* is lower when the wind is stronger, but it also could be possible that the vocalizations were masked by the sound of the wind. Wind is the principal source of low-frequency noise (Brumm & Slabbekoorn, 2005) and it is well known that it affects recordings obtained with omnidirectional microphones (Agranat, 2009). Wind has been identified as the most important cause of misdetection of birds in acoustic automatic recognition systems (Digby et al, 2013). Noise generated by wind affects mostly low frequencies, generally below 2 kHz due to its interaction with the vegetation in terrestrial environments (Buscaino et al, 2014). Thus, a possible solution could be to remove the unwanted sounds with a low-pass filter before analysis (Agranat, 2009). To avoid wind interferences in the cross-correlation detection method, another solution would be to specify the bandwidth of the template, thus discarding the sounds below or above the specified frequencies. Nevertheless, the frequency values of *P. mocinno* vocalizations are relatively low (between 0.5 and 2 kHz), partially falling into the spectrum of the wind. Consequently, only the frequencies below 0.5 kHz were not taken into account for the detection process and wind noise overlaps with the vocalizations of *P. mocinno*, affecting the automatic detections.

Most of detections of *P. mocinno* vocalizations were obtained in days of high cloudiness. It is known that *P. mocinno* is more active in cloudy weather than when the sunlight incidence is direct (LaBastille et al, 1972; Monge-Najera & Hernandez, 1994). Iridescence of the feathers of *P. mocinno* is linked to light incidence, being more brilliant in direct light (Durrer & Villiger, 1966; LaBastille et al, 1972; Monge-Najera & Hernandez, 1994). Thus, these studies support the hypothesis that the plumage of *P. mocinno* is probably intended to a camouflage in wet or rainy weather conditions, when the species is more active. In contrast, in direct sunlight the iridescence of the green feathers makes the individual bright and conspicuous, and individuals are less active. Therefore we can expect that *P. mocinno* is also more active vocally when the weather is cloudy, as suggested by the results of the mixed model.

By this research, we demonstrate the high potential of acoustic detection methods, for long term monitoring of *P. mocinno* in its habitat. Problematic bird species, causing false positives have been identified, which gives an opportunity to improve the cross correlation method in future studies. The actual range of the automatic detection of *P. mocinno* by cross-correlation in recordings obtained by autonomous recorders, was

determined. Knowing the detection range is valuable to design a proper sampling protocol for future studies. Changes in acoustic activity of *P. mocinno* detected along different years of a monitoring program can be explained the weather. Influence of weather on fluctuations of automatic detections must be taken in consideration for the interpretation of results.

3.6 Acknowledgements

We thank Los Andes reserve for the hospitality and support of its staff during the field survey. We also thank Jesús Lucas and Selvin Xiloj for guiding us in the field and share their knowledge. Also thanks to Amandine Blin for the advice on statistics. We would like to thank Juan S. Ulloa and Manon Ducrettet for their valuable comments and suggestions. This work was funding by the National Geographic Society [grant number 9479-6].

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Chapter 4: Acoustic competition within a bird community: the case of the Resplendent Quetzal (*Pharomachrus mocinno*)



Chlorophonia occipitalis in the south slope of volcano Atitlán (Picture: Pablo Bolaños)

4.1 Summary

4.1.1 Context

Species in a community compete for resources. One special case of ecological resource is the “acoustic space”. It has been suggested that *P. mocinno* has strong competitors in its community, although the level of competition with the species have never been quantified.

4.1.2 Problematics

We aimed at estimating the level of competition of the Resplendent Quetzal with species belonging to the same acoustic community, which are sharing the same acoustic space.

4.1.3 Methods

Species sharing the frequency bandwidth with *P. mocinno* were identified. Each species that potentially overlaps acoustically in time and frequency with *P. mocinno* vocalizations was identified. The potential overlap between *P. mocinno* and the other species in the acoustic community was quantified and compared with the actual acoustic overlap. Multivariate analysis was conducted taking in consideration several competition traits and the phylogenetic distance, to better identify the species competing the most with *P. mocinno*.

4.1.4 Main results

The acoustic overlap between *P. mocinno* and the other species in the acoustic community was generally high with species competing for food resources. The acoustic overlap was low with predator species of *P. mocinno*. The strongest competitor with *P. mocinno* was *T. mexicanus*, a species closely related phylogenetically.

4.1.5 Perspectives

The results presented here can be useful as a base to conduct other specific studies in the community of *P. mocinno*. The analysis presented here focused on *P. mocinno*, but similar analysis should be done for the competing species to obtain a better image of the interactions between all species. The same methodology can be applied to other communities and animal groups, in order to tackle important ecological problems, like acoustic niche, changes due to migratory or invasive species, or response of acoustic indices.

4.1.6 Related communications and publications

Acoustic monitoring of *Pharomachrus mocinno*, Resplendent Quetzal, a flagship bird species of Guatemala. Bolaños, P., Sueur, J., Aubin, T. Poster presentation at the African Bioacoustics Community Conference, 2018. Cape Town, South Africa.

Supervision of a Biology license thesis of the “University del Valle de Guatemala”. The student Andrea Padilla conducted her thesis using our recordings. Part of her thesis required manual selection of vocalizations in the recordings. These selections were used in the chapter four of this PhD thesis, in order to study the acoustic community of *P. mocinno*.

4.2 Introduction

In an animal community, interspecific competition mainly refers to a mutually negative interaction between two or more species. The inter-specific competitive interactions may reduce survivorship, abundance, fitness, or a fitness component, such as body size, growth rate or fecundity. In mobile species, like birds, the competition is driven by the access to resources (Morin, 2011). Food, sexual territory, or nest sites are identified as the main resources structuring communities through competition.

A particular case, rarely considered, is the acoustic resource shared by several species producing sound and constituting therefore an acoustic community (Farina & James, 2016; Gasc, Sueur, Pavoine, Pellens, & Grandcolas, 2013). An acoustic community can be defined as a collection of sounds produced by living organisms occurring in a given habitat over a specified time (Gasc et al., 2013). Studying the acoustic community dynamics is a valuable tool to understand what drives changes in community composition and species abundance (Lellouch, Pavoine, Jiguet, Glotin, & Sueur, 2014).

Competition between species and habitat-dependent selection pressure are two mechanisms that may shape phenotypic traits between and within species (Lankau, 2011). The structure of an acoustic community could be ruled out by the occurrence of species-specific acoustic niches (Krause, 1993), a concept deriving from the classic Hutchinson niche concept (Hutchinson, 1959). According to the acoustic niche hypothesis (ANH), vocal species sharing the same acoustic space would avoid or reduce acoustic overlap. The ANH therefore predicts a frequency partitioning and/or a temporal partitioning (Farina, Lattanzi, Malavasi, Pieretti, & Piccioli, 2011).

Competition for acoustic space can be inferred from the importance of animal acoustic signals. In addition, acoustic interferences between species can be considered as

a competition as the acoustic space is a limited resource. Selection may then cause changes in the signal system or in the spatial distribution of signals. A hypothesis of signal space competition can be extended to community-wide patterns wherein signal space may be partitioned to minimize overlap among sympatric species, resulting in an over-dispersed or regular pattern (Chek, Bogart, & Lougheed, 2003). Acoustic partitioning through temporal and spectral features has been found among different animal taxa. Temporal and frequency acoustic partitioning have been found in amphibian territorial vocalizations, which attract conspecific females (Garcia-Rutledge & Narins, 2001; Hodl, 1977; Villanueva-Rivera, 2014). Frequency and temporal acoustic partitioning has been observed as well in fish (Parsons, McCauley, & Thomas, 2013; Ricci, Eggleston, & Bohnenstiehl, 2017). Acoustic partitioning has also been found in arthropods, like orthopterans (Latimer & Broughton, 1984; Schmidt & Balakrishnan, 2014) and cicadas (Sueur, 2002). In birds, acoustic partitioning has been studied extensively, suggesting temporal and frequency acoustic partitioning among bird communities (Azar & Bell, 2016; Brumm & Slabbekoorn, 2005; Farina et al., 2011; Planqué & Slabbekoorn, 2008). Acoustic partitioning has also been reported in communities among different taxonomic groups (amphibians, birds and insects) (Aide, Hernández-Serna, Campos-Cerqueira, Acevedo-Charry, & Deichmann, 2017).

Individuals of different bird species can perform in strict coordination (Farina et al., 2011; Malavasi & Farina, 2013), with an emergent pattern which may well also act as a new signal, that could act as a joint resource defence. In cooperative association, birds could communicate information about group capabilities to non-group members, and vocalization patterns within the community could contribute to defining the species composition of the community itself. The longer that individuals share resources in the same environment, the more their fitness interests overlap to a considerable degree (Tooby & Cosmides, 1996).

Habitat-dependent selection pressure is another evolutionary mechanism that may shape phenotypic traits between and within species (Lankau, 2011). The structure of animal acoustic signals could be adapted for transmission through the habitat, so that divergence could be observed between populations inhabiting different habitats (Morton, 1975). Acoustic adaptation hypothesis (AAH), first suggested by Morton (1975), helps to explain variation in acoustic signal between populations differing in the environment structure of their habitats (Graham, Sandoval, Dabelsteen, & Mennill, 2017). Experiments of sound propagation clearly demonstrate the effects of the environment on acoustic structure (Wiley & Richards, 1978). Hence, in opposition to the ANH, the AAH leads to

predict a convergence of sounds produced by species sharing the same habitat and same time of singing. However variation in acoustic structure of vocal signals in a community seem to be dependent at the same time, on the species, the environment and the function of the calls considered. Predictions for environmental influences on vocal behaviour should therefore be adapted to the peculiarities of the vocalizations under study, the study species and its environment (Ey & Fischer, 2009).

The cloud forest is one of the most endangered habitat types in tropical regions (Pope & Harbor, 2014). The cloud forest provides unique habitat for endemic species of birds and other animal species (Eisermann & Avendaño, 2008). One important bird species restricted to the cloud forest of south of Mexico and Central America is *Pharomachrus mocinno*, which is considered in Guatemala as an endangered species (CONAP, 2009) and as near threatened in the red list of endangered species of the International Union for Conservation of Nature (IUCN) (Birdlife International, 2016). *P. mocinno* occupies a central place in the Guatemalan culture, being a flagship for conservation of the cloud forest habitat and the species occurring there. In addition, the species is a key for the regeneration of the cloud forest, being a seed disperser of at least 32 plant species (Avila, Hernández, & Verlarde, 1996). *P. mocinno* does vertical migrations between low to high altitude sites according to the fructification of the plant species it feeds on, in particular the tree family Lauraceae.

Pharomachrus mocinno competes with other species for ecological resources, as territory areas, nest sites and food (Santana & Milligan, 1984). The competition could be highly asymmetric with some species acting also as predators of *P. mocinno*. As other bird species, *P. mocinno* probably compete as well for an access to the acoustic space. Among the bird species living in the same area as *P. mocinno*, some of them emit vocalizations within the same frequency bandwidth, so they have the potential to overlap with *P. mocinno* vocalizations. Being the acoustic space a limited resource, the species might compete also for this resource in order to avoid interference (ANH), and the competition could be different according to the vocalizations and behaviour of each species.

Tropical bird species living in closed forest have relatively low pitched and long-drawn tonal note vocalizations, while species inhabiting more open habitats generally produce higher-pitched songs with repetitive trills of short and stereotypic notes (Morton, 1975). This pattern is observable even taking in consideration phylogenetic relationships and body size (Ryan & Brenowitz, 1985). However, according to the ANH, species vocalizing at similar frequency ranges, may have fitness costs due to interference

affecting species recognition, and this could cause some species to avoid vocalizing when other species using the same frequency range, also vocalizing. Therefore, bird species vocalizing at similar frequencies could have significantly less acoustic overlap in time, than between species vocalizing at different frequency ranges (Planqué & Slabbekoorn, 2008).

In order to describe and understand the acoustic community *P. mocinno* belongs to, and to better understand the acoustic competition that could occur between *P. mocinno* and other bird species living in the same cloud forest, an acoustic survey was conducted during 17 consecutive days with automatic recorders. Species sharing the frequency bandwidth with *P. mocinno* were identified in the resulting recordings and the potential and the observed acoustic overlap between vocalizations of *P. mocinno* and of other species was estimated. A multivariate analysis was conducted taking in consideration not only the acoustic overlap, but also the phylogenetic distance, and several competition traits to better identify the species competing the most with *P. mocinno*.

4.3 Material and methods

4.3.1 Study site and data collection

Field work was conducted at “Los Andes”, Suchitepéquez (14° 54' - 91° 18', 1661 m.a.s.l.). “Los Andes” is a private reserve including 607 ha on the southern slope of the Atitlán volcano at an elevation of 840 – 1830 m.a.s.l. “Los Andes” is covered by cloud forest on the highest part of the reserve (364 ha) and crops of coffee, tea and rubber on the lowest part (243 ha).

Soundscapes of the cloud forest where *P. m. mocinno* is known to occur were recorded using automatic recorders Wildlife Acoustics® SM2 at four simultaneous sites. The recorders were separated with by an average of 450 m between each other so that their area of recording did not overlap avoiding pseudo-replication (Figure 47). The recorders were programmed to record continuously from 5:00 to 9:30 am and from 15:30 to 18:00, when most of bird species are active that is around the dawn and dusk choruses. Recordings were split into 30 min files, so that 778 files were obtained. The recorders worked during 17 days in 2016 (February 8-25). Recordings were taken at a sampling frequency of 44.1 kHz and a dynamic depth of 16 bits with the internal omnidirectional microphones that have a frequency response between 0.02 and 20 kHz.

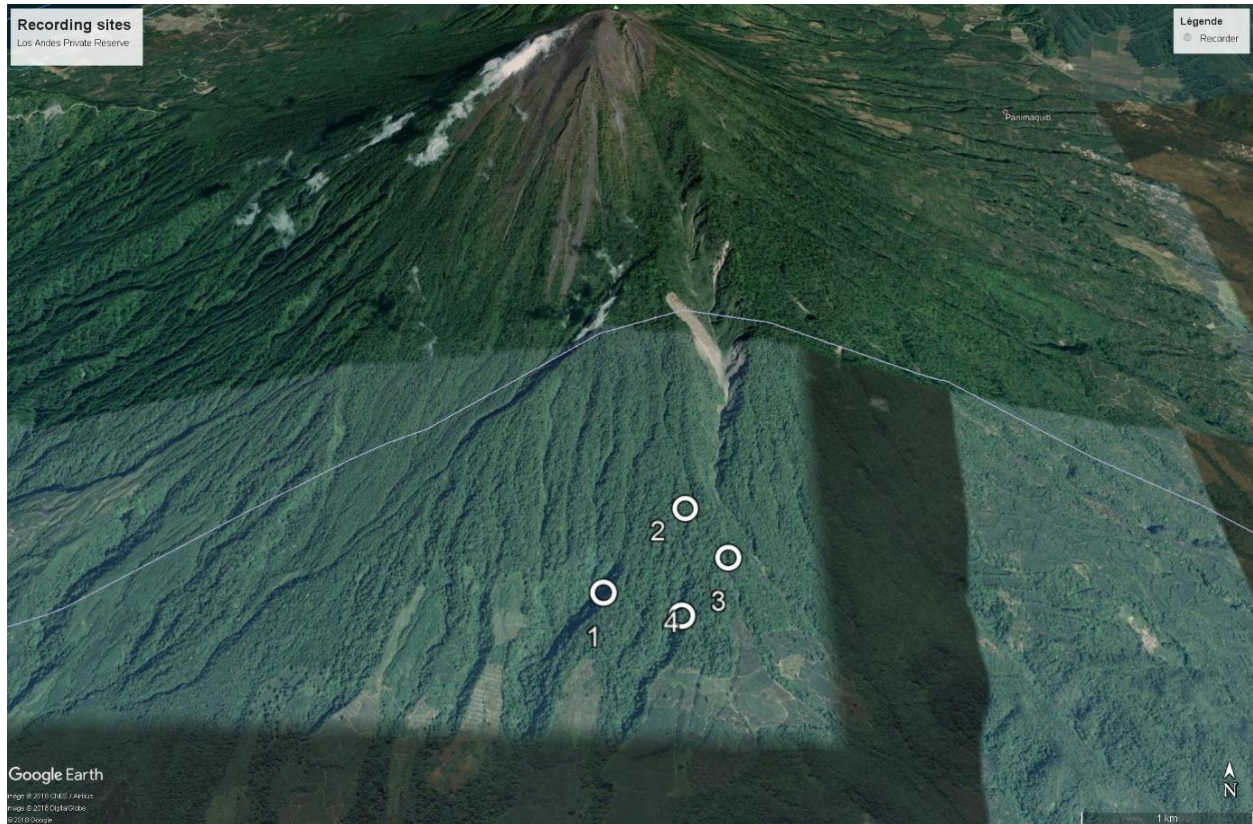


Figure 47: Recording sites in Los Andes reserve, on the south slope of volcano Atitlán, Guatemala (Google Earth view)

4.3.2 Data analysis

The vocalizations of *P. mocinno* were manually searched by hearing and on-screen observations in the recordings (time precision = 0.0232 s, frequency precision = 21.5 Hz). *P. mocinno* was detected in 93 recordings among the 778 recordings. A random subsample of 48 recordings from these 93 recordings was built to analyze the acoustic competition of *P. mocinno* with other species.

All the vocalizations of *P. mocinno* in the 48 recordings were manually annotated and classified as territorial, alarm, or courtship vocalizations. The vocalizations of all other species which occur in the same bandwidth between 0.5 and 2.5 kHz and within 300 s before, during or after a vocalization of *P. mocinno* were similarly annotated. Annotations were added with Raven Pro 1.5 software (www.birds.cornell.edu/raven) directly from on-screen measurement cursors on the spectrogram (time precision = 0.0232 s, frequency precision = 21.5 Hz).

Selections were made taking the duration (s) and the highest and lowest frequencies (Hz), resulting in time x frequency rectangles (Figure 2).

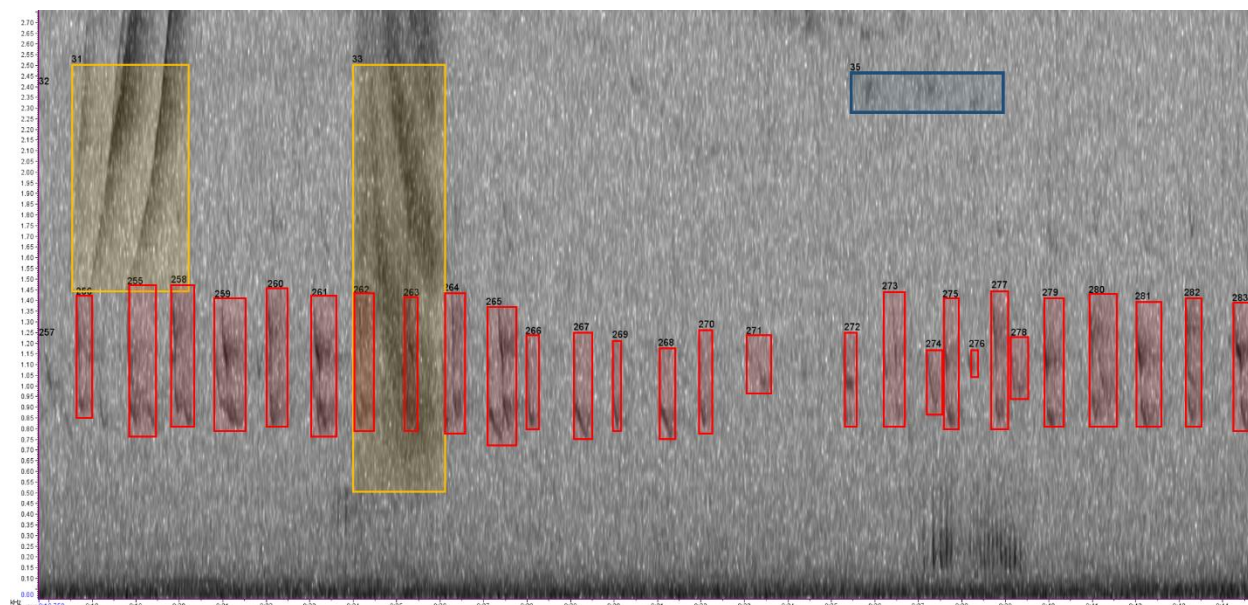


Figure 48: Manual selections of vocalizations. Manual selections were made using the spectrogram display of Raven Pro 1.5 software with a time precision = 0.0232 s and frequency precision = 21.5 Hz. All the vocalizations found within 300 s before, during or after a vocalization of *P. mocinno* were manually selected. Selections were made taking the duration (s) and the highest and lowest frequencies (kHz), between 0.5 and 2.5 kHz, resulting in rectangles with x and y coordinates (respectively time and frequency). Vocalizations numbers 256-283 (red rectangles) were produced by *P. mocinno*, vocalizations number 31 and 33 (yellow rectangles) by *P. nigra* and vocalization number 35 (blue rectangle) by *M. occidentalis*

To test the acoustic overlap between *P. mocinno* and the other species, the overlap in frequency and time was quantified by estimating the percentage of the time x frequency area of the *P. mocinno* vocalizations overlapped with the vocalizations of other species (Figure 49). For each species, an overlap rate was quantified as the sum of all the overlap percentages between the species and *P. mocinno*, divided by the times that *P. mocinno* vocalized. In addition, the maximum acoustic overlap with *P. mocinno* vocalizations that each species has (potential overlap) was quantified according to the average frequencies of their vocalizations in relation to those of *P. mocinno*. Then a comparison between the overlap rate (observed) and the potential overlap was made by subtracting the later value to the former, for each species. This calculation made possible comparisons of the actual acoustic overlap with *P. mocinno* vocalizations among the different species.

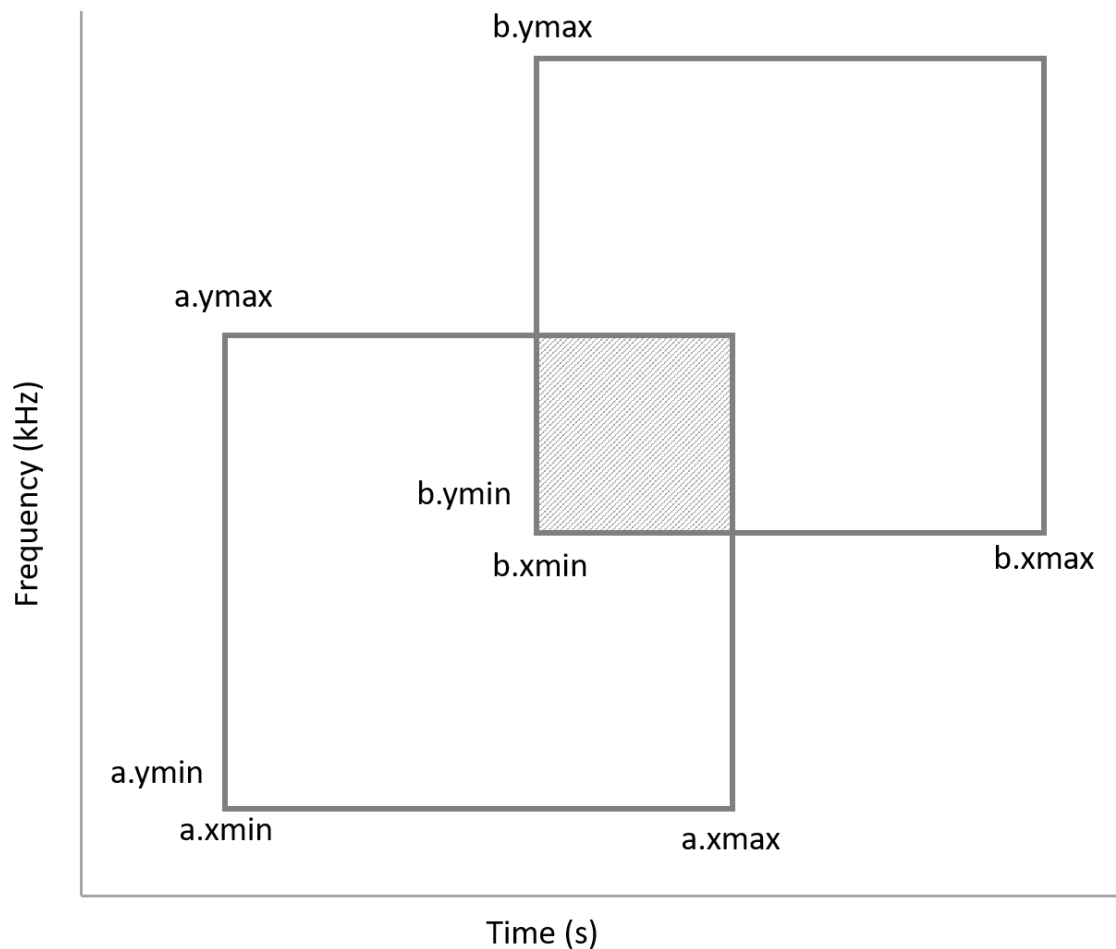


Figure 49: Diagram showing the overlap calculation between *P. mocinno* (species a) and the other species (species b) vocalizations. The grey zone represents the overlapping area between the two species. The overlapped area was calculated as a percentage of the overlapped area in relation to the total area of *P. mocinno* vocalization that is, in this case, $100 * (|a.xmax - b.xmin| * |a.ymax - b.ymin|) / (|a.xmax - a.xmin| * |a.ymax - a.ymin|)$

Competition for other resources was also taken into account. The following competition traits were considered: food, nest type, singing time of day, breeding period in the year, and predation. The information about non acoustic resource used between each species and *P. mocinno*, for feeding, nesting type and singing time of day, was encoded as 1 if it was the same, or 0 if the use was different. For the breeding period, the information was encoded as the number of months that the species coincide with the breeding period of *P. mocinno*. This number of was scaled between 0 and 1, with 0 indicating no overlap in the breeding season and 1 a total overlap. Possible predation of adults, chicks or eggs of *P. mocinno* was encoded for each species as 1 if it is known to

occur and 0 if not. The data was obtained from personal observations, experts (Dallies *com pers*) and literature (Avila et al., 1996; BirdLife International, 2017; Bustamante, Barrios, & Juárez, 2010; Carroll, Kirwan, & Boesman, n.d.; Collar, 2017; Collar & Christie, 2017; Eisermann, Komar, & Herrera, 2006; Fagan & Komar, 2016; Foster, 2007; Haverschmidt, 1962; Howell & Webb, 1995; Johnsgard, 2000; Miller, Greeney, & Valdez, 2010; Motta, 2007; Santana & Milligan, 1984; Snow, 2001; Solórzano, Castillo, Valverde, & Avila, 2000; Specht, Mesquita, & Santos, 2008; Thorstrom, 2000; Wenny, 2014; Zimmer & Isler, 2003),.

In addition, median phylogenetic distance between the Resplendent Quetzal and the other species was added as millions of years of the most recent common ancestor (MRCA), using the tool for its calculation in TimeTree (<http://www.timetree.org>). When one or both of the species were not present in TTOL, the next higher taxa was taken. Then, those taxa were used as proxies to find the MRCA for the given query. Finally, the divergence time for the MRCA was retrieved from the TimeTree database.

4.3.3 Statistical analysis

The combination of all competition variables led to a matrix made by 16 rows (species) and nine columns (difference between the observed and the potential overlap with three vocalization types of *P. mocinno*, five resource competition and the phylogenetic distance) (Table 9).

This competition matrix was treated with a principal component analysis (PCA). The species were used as an explained (dependent) variables; the competition for the acoustic space, the competition for ecological resources and the phylogenetic distance were included as explaining (independent) variables. The PCA was conducted (1) to identify inter-correlations between the acoustic overlap and the competition for other ecological resources between *P. mocinno* and the other species, (2) to analyse possible inter correlations between the acoustic overlap and phylogenetic distance, and (3) to reveal the most important competitors with *P. mocinno*.

Table 9: Competition for resources, and phylogenetic distance between *P. mocinno* and the other species included in the analysis. Resource use comparison between *P. mocinno* and the other species was encoded as: 1=same use, 0=different use. Possible predation of *P. mocinno* was encoded as: 1=known to occur, 0=not predator or not known to occur. Breeding overlap was encoded between 0 and 1 as a rate of

overlapping months with the breeding period of *P. mocinno* (i.e. 1 = full overlap for the 4 months of the breeding period). Phylogenetic distance was included as the estimated median time in millions of years of the most recent common ancestor (MRCA) (www.timetree.org). Obs-pot overlap: refers to the difference between the observed and the potential overlap respectively for the territorial, courtship and alarm vocalizations of *P. mocinno*

Species	Same food	Same nest	Singing time	Predation	Breeding period	Phylogenetic distance	Obs-pot overlap territorial	Obs-pot overlap courtship	Obs-pot overlap alarm
<i>A. gularis</i>	0	0	1	0	0.75	73	-0.26	-0.31	-0.32
<i>A. prasinus</i>	1	1	0	1	1	69	-0.76	0.17	-0.22
<i>C. ustulatus</i>	1	0	1	0	0.75	81	0.07	0.01	0.48
<i>C. occipitalis</i>	0	0	0	0	0.5	81	0.00	0.01	-0.65
<i>C. melanocyaneus</i>	1	0	0	0	0.5	81	0.00	0.00	0.14
<i>G. brasilianum</i>	0	1	1	0	1	78	-0.10	-0.57	-0.19
<i>H. leucophrys</i>	0	0	0	0	1	81	0.00	0.00	-0.15
<i>H. cachinnans</i>	0	0	1	1	0.5	80	-0.27	-0.02	-0.34
<i>M. ruficollis</i>	0	0	0	1	1	80	-0.89	-0.84	-0.73
<i>M. occidentalis</i>	1	0	0	0	1	81	0.00	0.00	0.46
<i>O. guttatus</i>	0	0	1	0	0.5	91.6	-0.94	-0.28	-0.43
<i>P. purpurascens</i>	1	0	1	0	1	91.6	-0.94	-0.03	-0.49
<i>P. nigra</i>	1	0	1	0	0.75	91.6	0.01	0.02	0.04
<i>T. collaris</i>	1	1	0	0	0.5	29	0.00	0.00	-0.42
<i>T. mexicanus</i>	1	1	0	0	0.5	29	0.15	0.05	-0.20
<i>X. erythropygius</i>	1	0	1	0	0.5	81	0.01	0.04	-0.48

4.4 Results

In total, 7806 vocalizations were identified in a bandwidth between 500 and 2500 Hz, belonging to 18 species, with a cumulative duration of 9907.68 s.

The species identified were: *Aspatha gularis* (Momotidae), *Aulacorhynchus prasinus* (Ramphastidae), *Catharus ustulatus* (Turdidae), *Chlorophonia occipitalis* (Fringillidae), *Ciccaba virgata* (Strigidae), *Cyanocorax melanocyaneus* (Corvidae), *Glaucidium brasilianum* (Strigidae), *Henicorhina leucophrys* (Troglodytidae), *Herpetotheres cachinnans* (Falconidae), *Micrastur ruficollis* (Falconidae), *Momotus momota* (Momotidae), *Myadestes occidentalis* (Turdidae), *Odontophorus guttatus* (Odontophoridae), *Penelope purpurascens* (Cracidae), *Penelopina nigra* (Cracidae), *Trogon collaris* (Trogonidae), *Trogon mexicanus* (Trogonidae) and *Xiphorhynchus erythropygius* (Furnariidae).

The species that overlapped the most with *P. mocinno*, regardless their potential overlap, were *C. ustulatus*, *A. prasinus*, *T. mexicanus*, *P. purpurascens*, *M. occidentalis*, *P. nigra* and *M. ruficollis*. Among these species, the most acoustically active ones were *T. mexicanus*, *C. ustulatus*, *M. occidentalis* and *M. ruficollis* (Figure 50).

The species vocalizations with the highest acoustic overlap with the territorial vocalizations of *P. mocinno* were *T. mexicanus*, followed by *M. ruficollis* and *C. ustulatus* (Figure 51). The species vocalizations with the highest acoustic overlap with the courtship vocalizations of *P. mocinno* were *P. purpurascens*, *A. prasinus*, and *M. ruficollis* (Figure 52). The alarm vocalization of *P. mocinno* was the most overlapped with the vocalizations of the other species, being *C. ustulatus* the species with the highest acoustic overlap with this vocalization type, then *A. prasinus*, *M. occidentalis*, *T. mexicanus* and *P. nigra* (Figure 53).

According to the average frequency bandwidth of the vocalizations of each species studied, the species that had the highest potential to overlap with the territorial vocalization of *P. mocinno* were *M. ruficollis* (100%), *P. purpurascens* (100%) and *O. guttatus* (94%) (Figure 54). The species with the highest potential to overlap with the courtship vocalization of *P. mocinno* were *M. ruficollis* (96%), *G. brasilianum* (57%) and *P. purpurascens* (42%) (Figure 55). The species with highest potential to overlap with the alarm vocalization of *P. mocinno* were *C. occipitalis* (96%), *M. ruficollis* (92%) and *A. prasinus* (80%) (Figure 56).

The species that had the highest observed overlap than the potential overlap with *P. mocinno* were *T. mexicanus* and *C. ustulatus* for the territorial vocalization (Figure 57); *A. prasinus*, *T. mexicanus*, and *X. erythropygius* for the courtship vocalization (Figure 58); and *C. ustulatus*, *M. occidentalis*, *C. melanocyaneus* and *P. nigra* for the alarm vocalization (Figure 59). The other species had an observed acoustic overlap similar or lower than the potential overlap (a difference between -0.04 and 0.04).

The first three axes of the PCA explained 67.94% of the variation in the competition of *P. mocinno* with the other species (Figure 60 and Table 10). For the first axis, the most important variables were the difference between the observed overlap and the potential overlap, with the territorial vocalization of *P. mocinno*, then with the courtship vocalization, and then the competition for food resources. For the second axis, the most important variable was the competition for the same nest type and the phylogenetic distance (Figure 61).

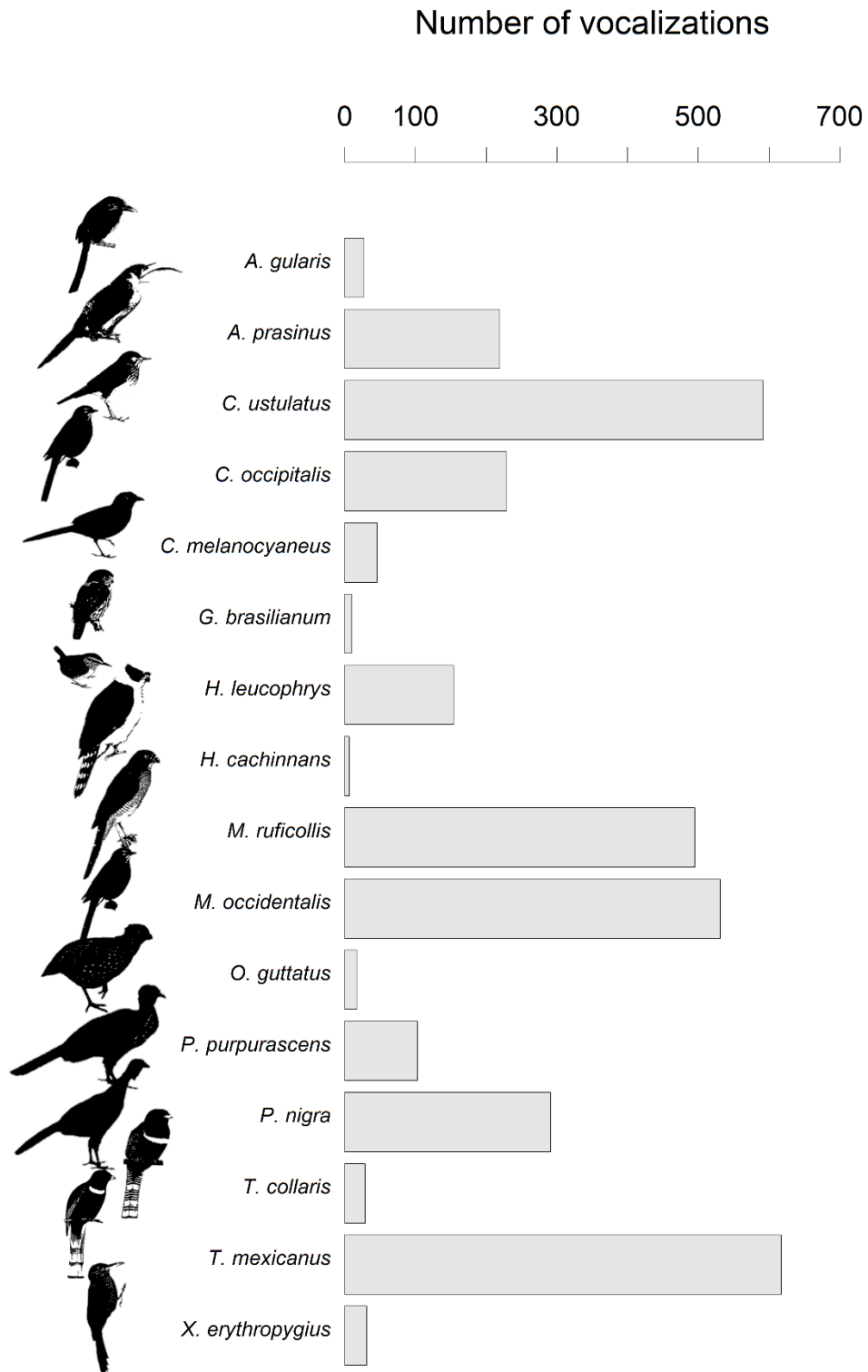


Figure 50: Number of vocalizations per each species. The raw number of vocalizations identified in the dataset. This number does not consider the overlap with *P. mocinno*, but only the abundance of vocalizations per species. See text for complete Latin names of the species

Table 10: PCA Axe coordinates of the different competition for resources. Obs-pot overlap refers to the difference between the potential overlap of one species to acoustically overlap with *P. mocinno* and the actual observed overlap.

Competition factor	PCA 1	PCA 2	PCA 3
Same food	-0.70	-0.12	-0.39
Same nest	-0.39	0.73	-0.13
Singing time	0.32	-0.57	0.26
Predation	0.47	0.48	-0.29
Breeding period	0.38	0.01	-0.82
Phylogenetic distance	0.61	-0.71	-0.17
Obs-pot overlap territorial	-0.75	-0.21	0.22
Obs-pot overlap courtship	-0.72	-0.23	-0.06
Obs-pot overlap alarm	-0.52	-0.51	-0.50

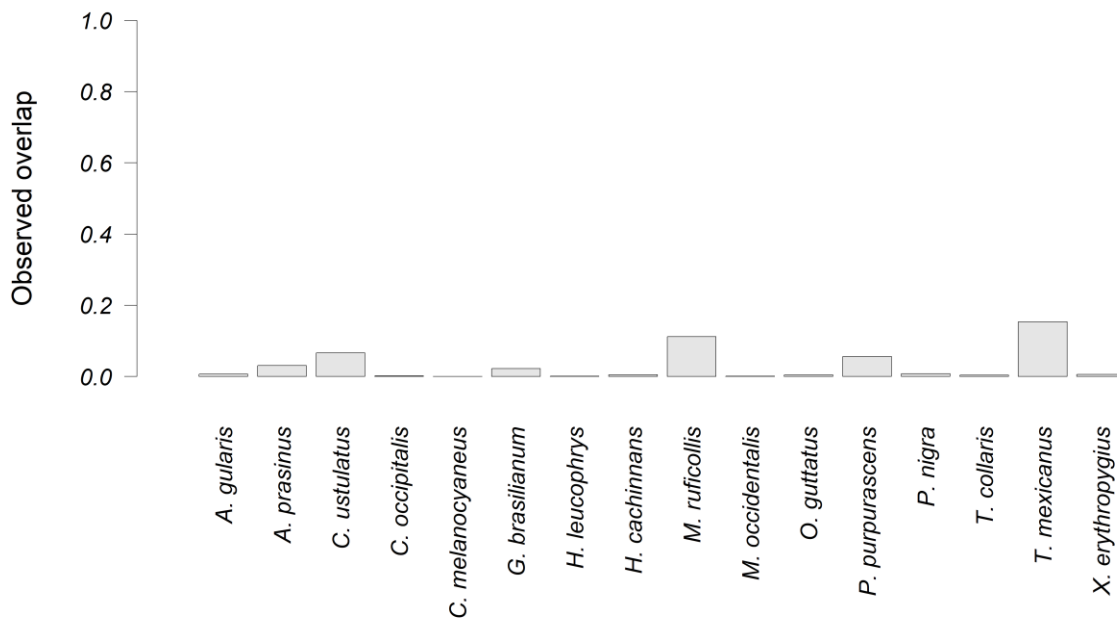


Figure 51: Observed overlap rate in frequency and time between the territorial vocalizations of *P. mocinno* and other species vocalizations. This observed overlap was calculated as the sum of the overlap percentage between *P. mocinno* and the other species, divided by the number of territorial vocalizations of *P. mocinno*

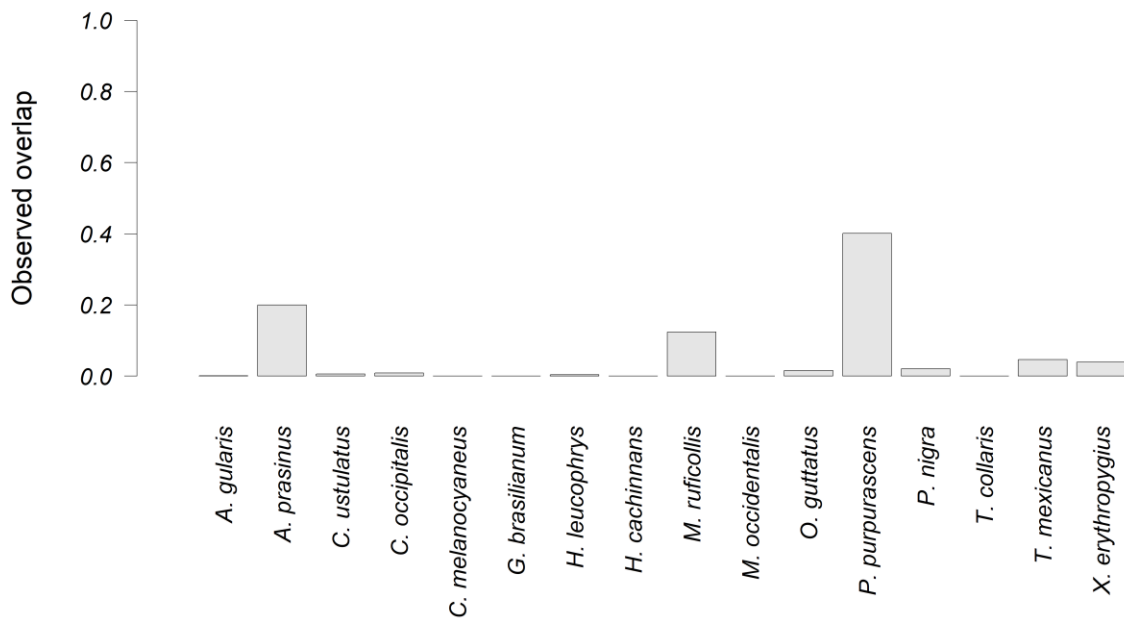


Figure 52: Observed overlap rate in frequency and time between the courtship vocalizations of *P. mocinno* and other species vocalizations. This observed overlap was calculated as the sum of the overlap percentage between *P. mocinno* and the other species, divided by the number of courtship vocalizations of *P. mocinno*

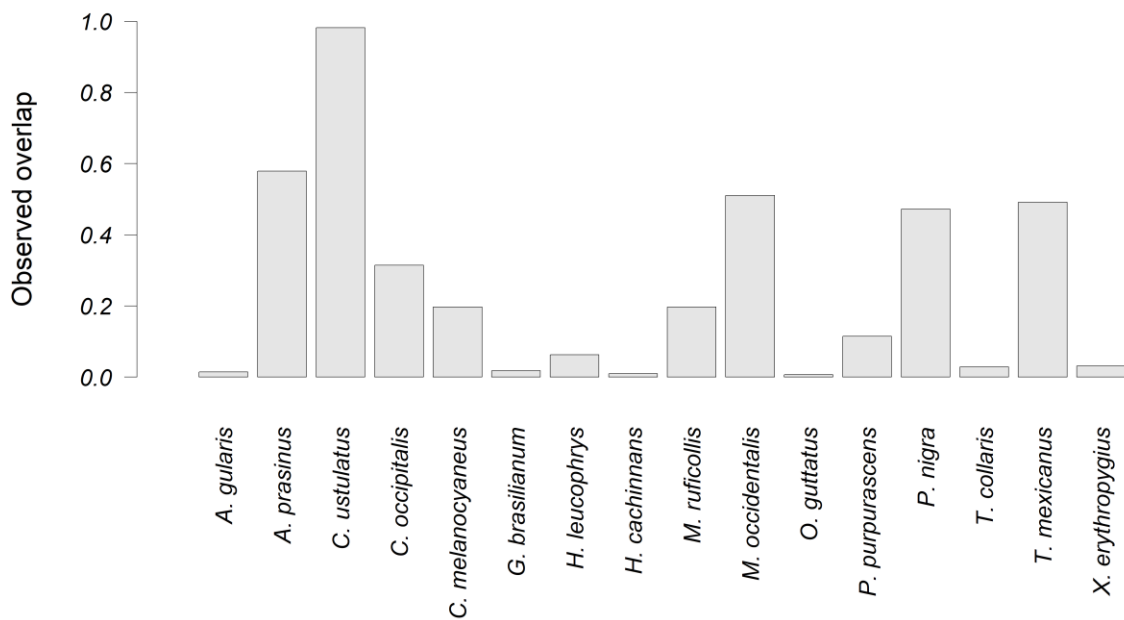


Figure 53: Observed overlap rate in frequency and time between the alarm vocalizations of *P. mocinno* and other species vocalizations. This observed overlap was calculated as the sum of the overlap percentage between *P. mocinno* and the other species, divided by the number of alarm vocalizations of *P. mocinno*

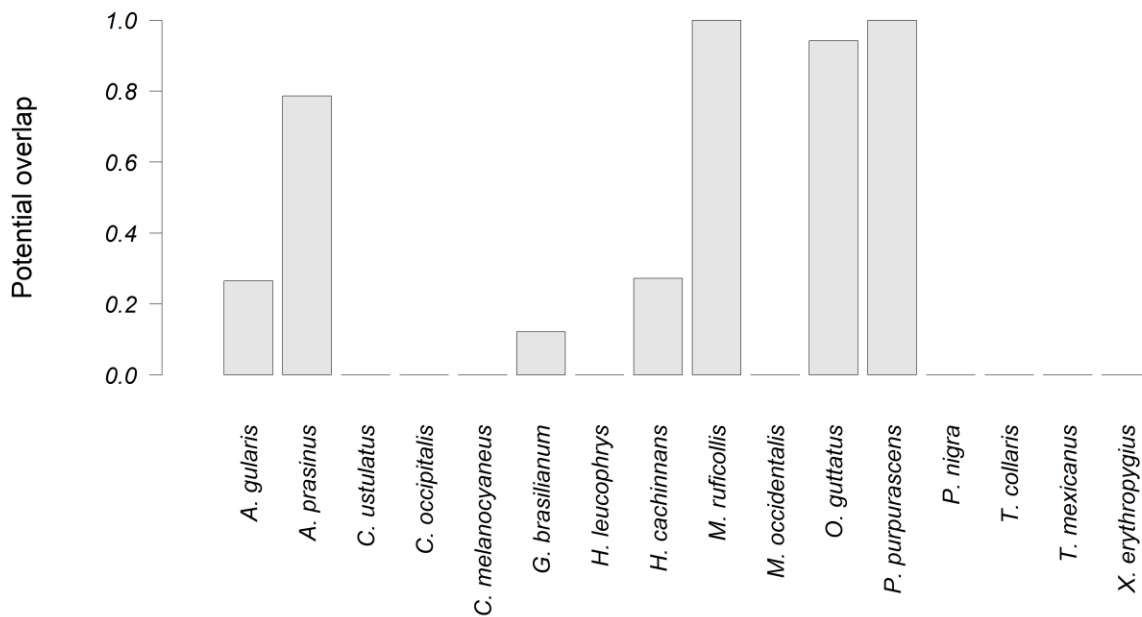


Figure 54: Potential overlap in frequency and time between the territorial vocalizations of *P. mocinno* and the other species. This potential overlap was calculated according to the maximum possible overlap between *P. mocinno* and other species vocalizations

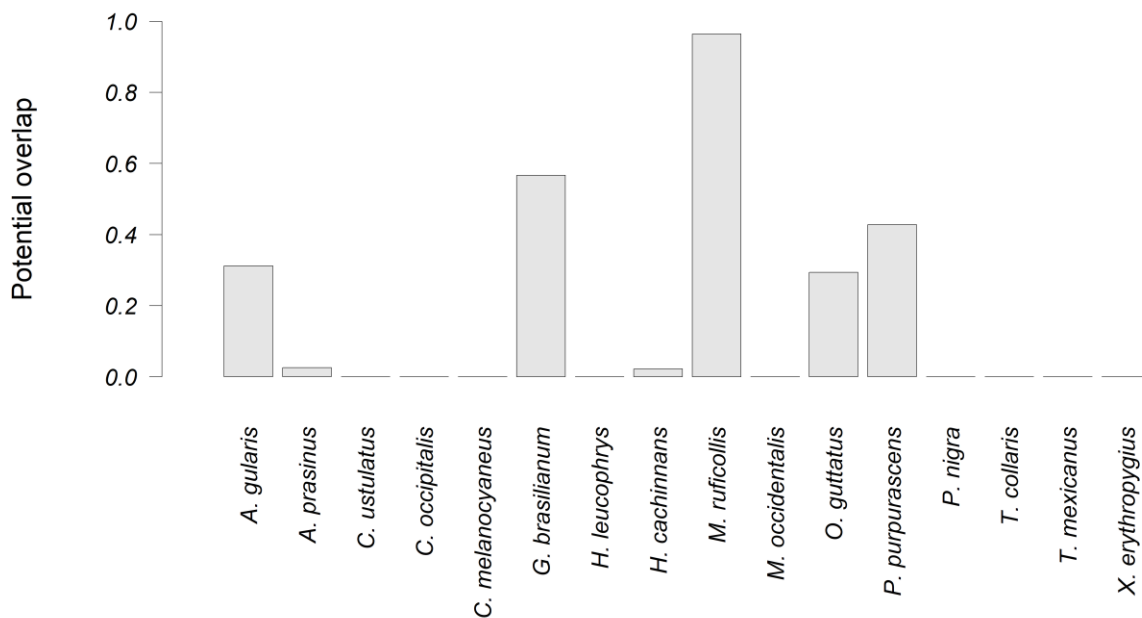


Figure 55: Potential overlap in frequency and time, between the courtship vocalizations of *P. mocinno* and the other species. This potential overlap was calculated according to the maximum possible overlap between *P. mocinno* and other species vocalizations

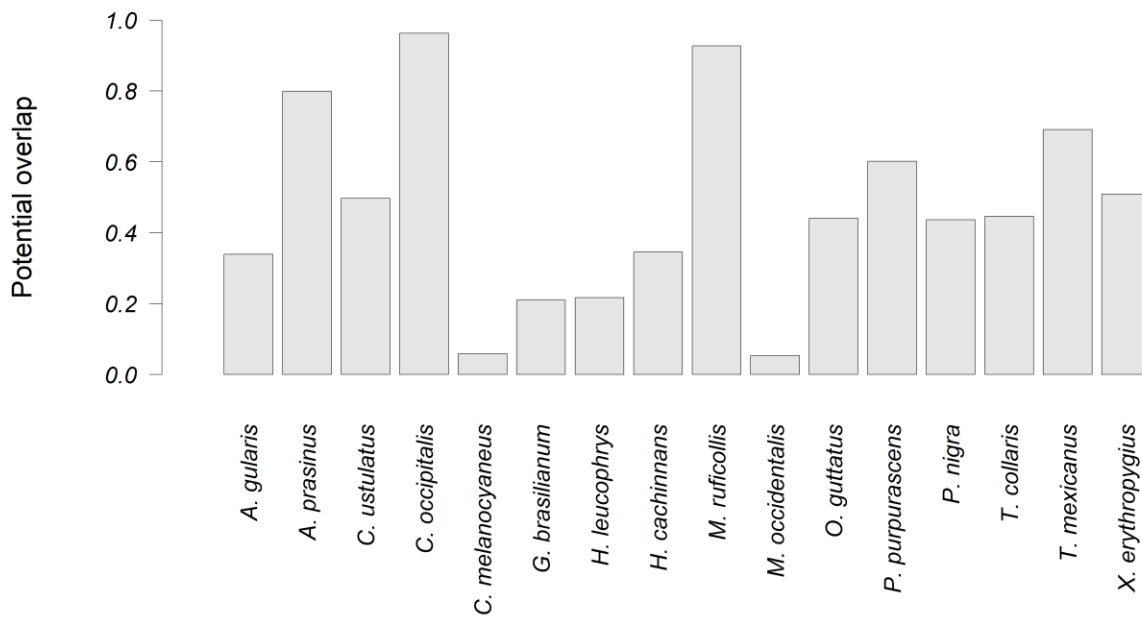


Figure 56: Potential overlap in frequency and time, between the alarm vocalizations of *P. mocinno* and the other species. This potential overlap was calculated according to the maximum possible overlap between *P. mocinno* and other species vocalizations

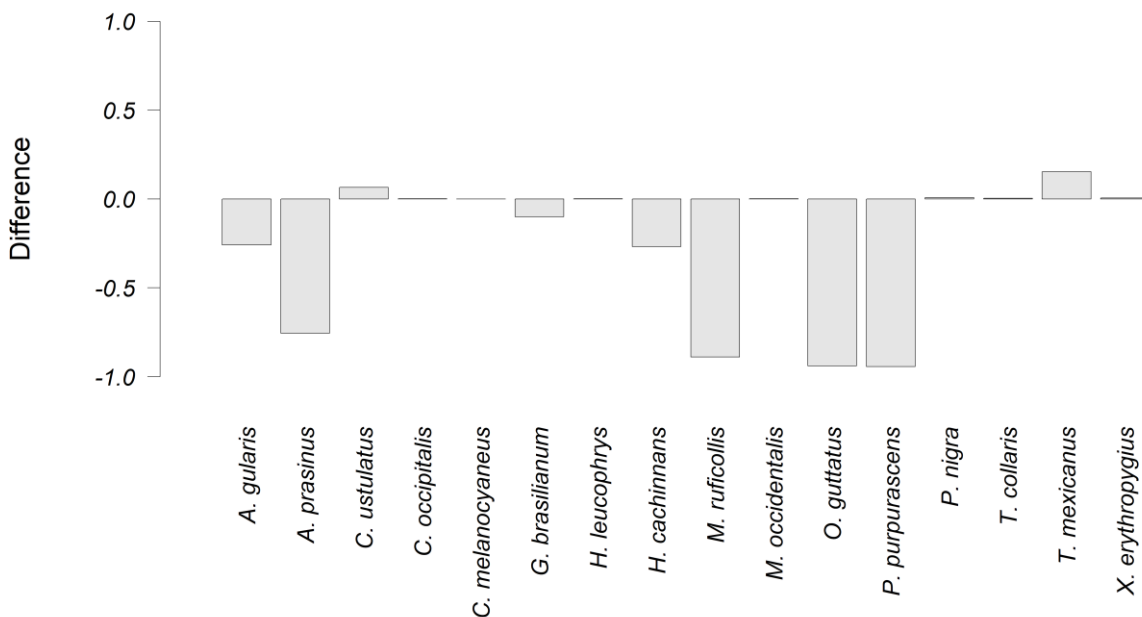


Figure 57: Difference between the observed overlap and the potential overlap of the territorial vocalizations of *P. mocinno* and other species vocalizations. A negative number means that the potential overlap is higher than the observed overlap. Conversely, a positive number means that the observed overlap is higher than the potential overlap

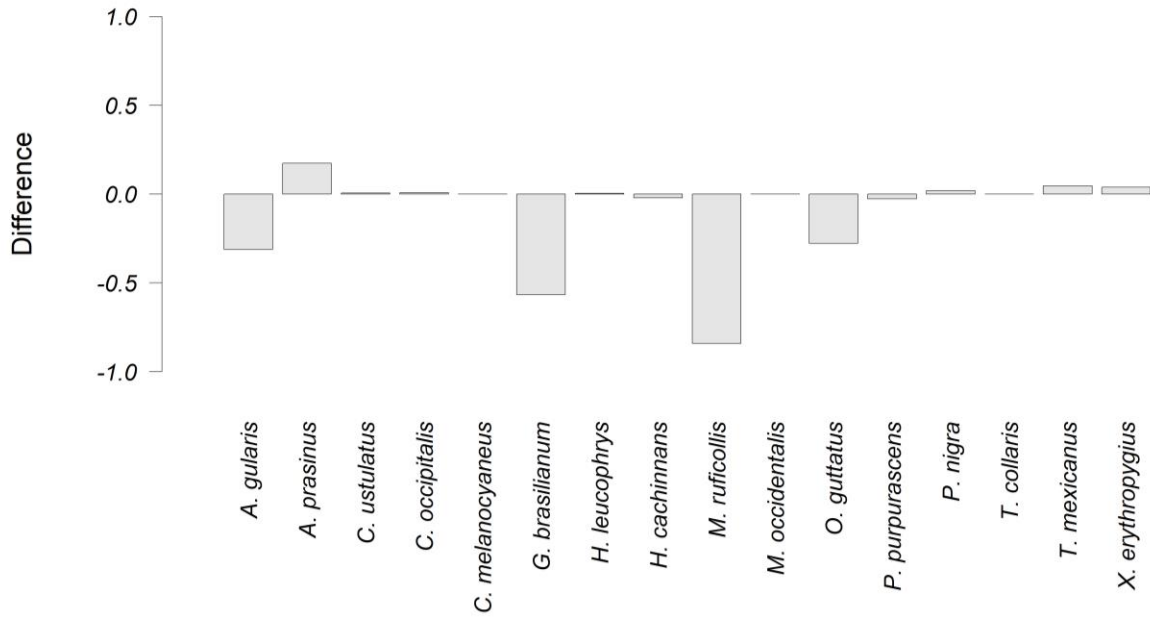


Figure 58: Difference between the observed overlap and the potential overlap, of the courtship vocalizations of *P. mocinno* and other species vocalizations. A negative number means that the potential overlap is higher than the observed overlap. Conversely, a positive number means that the observed overlap is higher than the potential overlap.

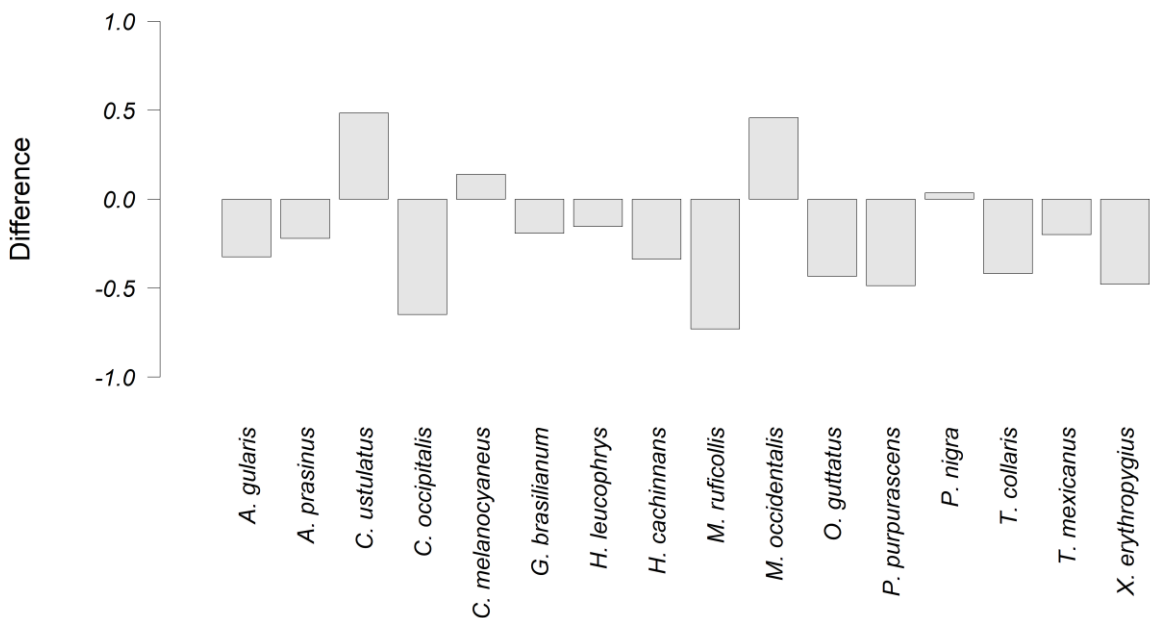


Figure 59: Difference between the observed overlap and the potential overlap, of the alarm vocalizations of *P. mocinno* and other species vocalizations. A negative number means that the potential overlap is higher than the observed overlap. Conversely, a positive number means that the observed overlap is higher than the potential overlap.

PCA analysis (Figure 62) revealed the following patterns of competition between the different species and *P. mocinno*: 1) Yellow species have an inter-correlation between the competition for food resources, and acoustic overlap with *P. mocinno* vocalizations; species in this pattern were *C. melanocyaneus*, *M. occidentalis*, *C. ustulatus*, *X. erythropygius* and *P. nigra*. 2) Red species, are phylogenetically close to *P. mocinno* use the same nest type, and had some overlap of their vocalizations with *P. mocinno*, in this pattern were observed *T. mexicanus* and *T. collaris*. 3) Blue species have an correlation between phylogenetic distance and time of day to vocalize; species phylogenetically distant to *P. mocinno* tend to vocalize at the same time of day, and their vocalizations had a low overlap with *P. mocinno*, in this pattern were observed *A. gularis*, *O. guttatus* and *P. purpurascens* 4) Purple species, is a predator that had a low acoustic overlap with *P. mocinno*, in this pattern only *M. ruficollis* was observed. 5) Grey species had a low acoustic overlap with *P. mocinno*, with low, or well partitioned ecological niches with it, namely *G. brasilianum*, *C. occipitalis*, *H. cachinnans*, and *H. leucophrys*. 6) Green species, is a predator with similar nest type than *P. mocinno*, and some acoustic overlap, in this particular case just *A. prasinus* was observed. 7) The only migratory species in the community analysed (*C. ustulatus*) had a high overlap with *P. mocinno*, the highest with the alarm vocalization and the second with the territorial vocalizations after *T. mexicanus*.

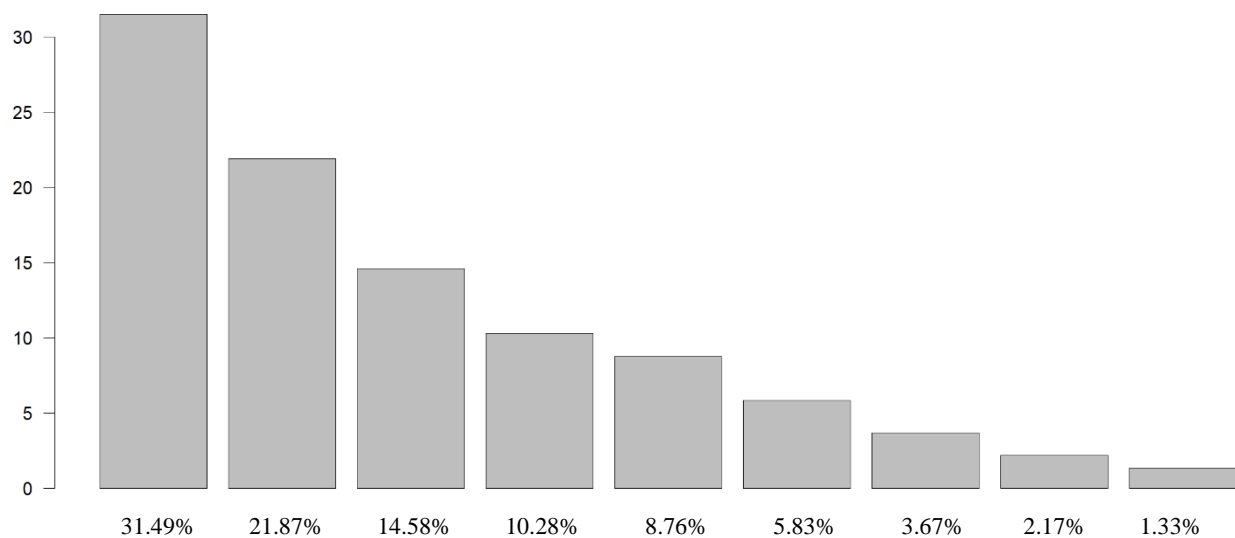


Figure 60: PCA analysis on competition for ecological resources: relative importance of the PCA axes. The first two axes explained 53.36% of variation for the competition of *P. mocinno* and other species

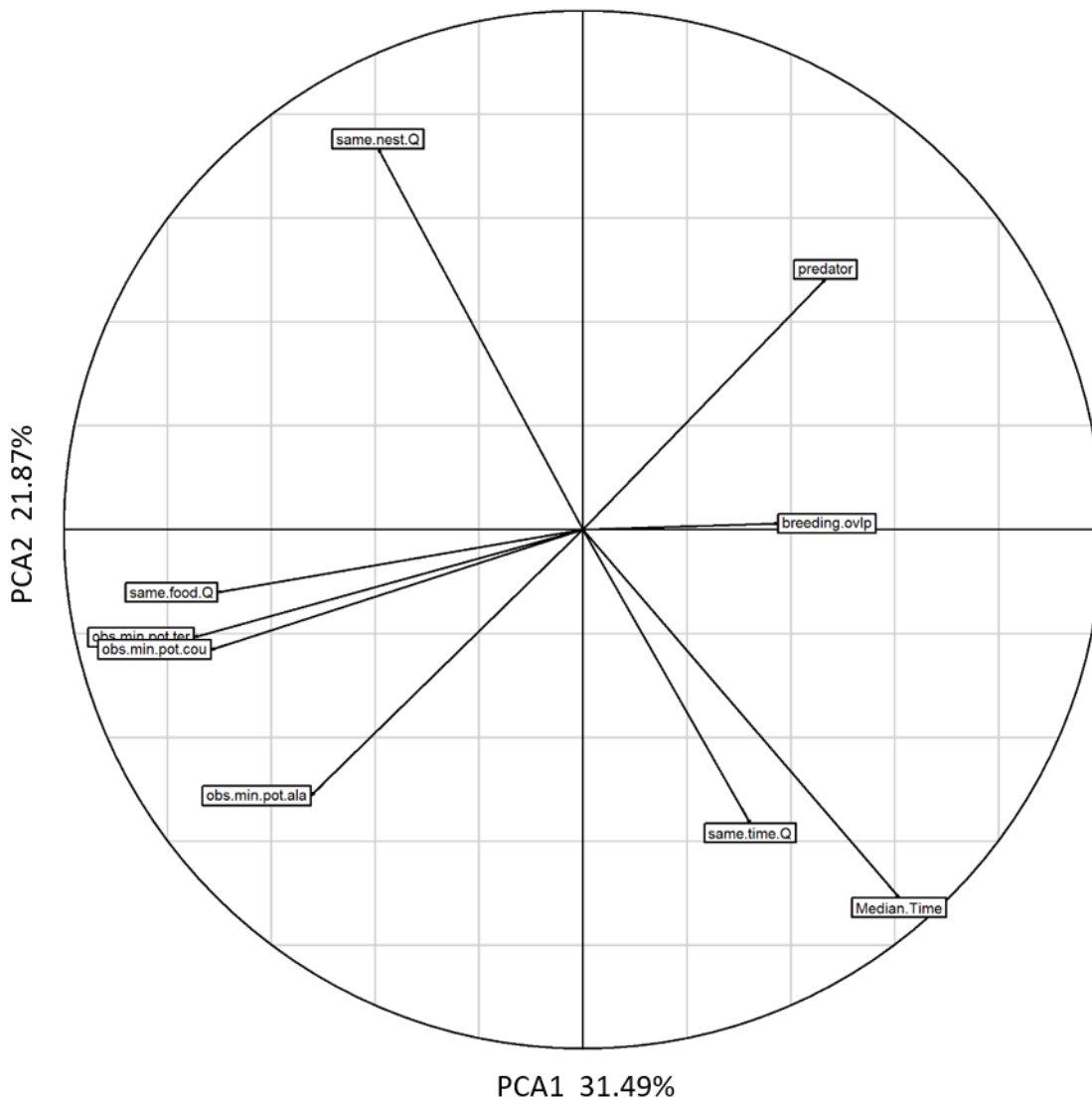


Figure 61: PCA analysis on competition for ecological resources: correlation circle. Correlation between the explaining variables according to the first two axes that explained 53.36% of the variation. obs.min.ter: difference between the potential acoustic overlap of a species and the observed overlap with the territorial vocalizations of *P. mocinno*; obs.min.cou: difference between the potential acoustic overlap of a species and the observed overlap with the courtship vocalizations of *P. mocinno*; obs.min.ala: difference between the potential acoustic overlap of a species and the observed overlap with the alarm vocalizations of *P. mocinno*; same.time.Q: same time of vocalizing in the day as *P. mocinno*; Median.Time: phylogenetic distance of a species with *P. mocinno*; breeding.ovlp: proportion of overlap of the breeding period of a species with the breeding period of *P. mocinno*; predator: possibility of predation of *P. mocinno* by a species; same.nest.Q: same nest type as *P. mocinno*

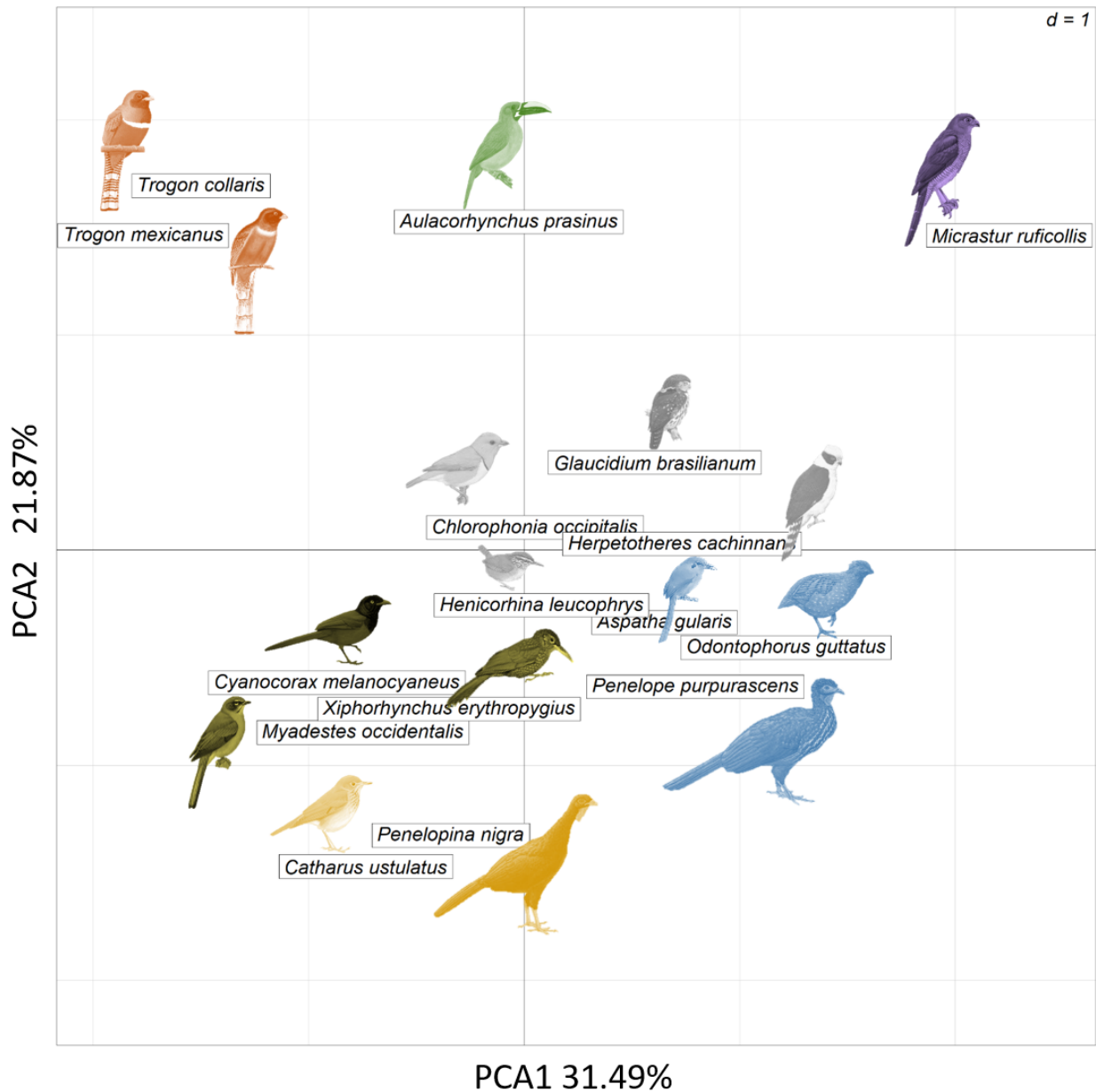


Figure 62: PCA analysis on competition for ecological resources: species plot. Individual plot with Species (individuals) placed in the PCA space according to the first two axes that explained 53.36% of the variation. Different colours highlight species of the different patterns of ecological competence mentioned in the text

4.5 Discussion

An analysis of the acoustic community of bird species vocalizing within the bandwidth of *P. mocinno* vocalizations was conducted in a fragment of cloud forest in Guatemala. The potential of each species of the community to overlap with the vocalizations of *P. mocinno*

was quantified and compared with the actual observed overlap with vocalizations of each species. A multivariate analysis was also conducted to assess the relative importance of several ecological traits, including acoustics, for the competition of *P. mocinno* with other species belonging to the same acoustic community.

The potential to overlap acoustically with *P. mocinno* differed between the species with, as expected, a higher overlap when the frequency bandwidths fell in the same range. Nevertheless, the observed overlap was not always related to the potential overlap. This difference could be due to the particular ecological interactions between *P. mocinno* and the other species, and not just to the acoustic characteristics of the vocalizations. Defining which species in the community competes the most for the acoustic space with *P. mocinno* needs to take into consideration several ecological and biological characteristics of the species. According to the different aggregations of species in the multivariate analysis done, different categories and patterns were identified. Among these general patterns, different competition categories were observed.

The first pattern identified was an inter-correlation between the use of the same food resources and a high acoustic overlap. The bird species in this category are completely or partially frugivorous, and not predators of *P. mocinno*, so they might compete with *P. mocinno* for food resources. In addition, species in this category are active approximately in the same forest strata. So the acoustic overlap could be due to disputes for food or space in the forest canopy. The acoustic strategy of *P. mocinno* might produce vocalizations to defend their surroundings at the risk of overlapping rather than to remain silent not to be detected by competitors.

Species phylogenetically close to *P. mocinno*, belonging to the same family Trogonidae, overlapped acoustically with *P. mocinno*. These related species could compete for nest sites and also for food resources. Phylogenetic history, reflect similarities in morphological and behavioural characteristics (Ryan & Brenowitz, 1985), so the acoustic overlap observed could be due in part, to morphological constraints. Defending nest areas and also competing for food might trigger the production of territorial vocalization and so acoustic overlap. Despite *T. mexicanus* has a low potential to overlap with territorial vocalizations of *P. mocinno*, *T. mexicanus* was the species which vocalization overlapped the most with the territorial vocalization of *P. mocinno*, among all the other species in the acoustic community. Production of territorial vocalizations are strongly dependent on the producers social and spatial relations, taking place during immediate competition over resources (Naguib, 2005). Thus, *T. mexicanus* could be the most important competitor in terms of acoustics with *P. mocinno*.

Phylogenetically distant species, namely *A. gularis*, *O. guttatus* and *P. purpurascens*, showed a low acoustic overlap with *P. mocinno* even if they vocalized at the same time of day. Luther (2009) suggested that acoustic partitioning among species singing in a short time interval is expected to be greater than the partition among species in the same community that usually sing in different space and time. Interestingly, the four species mentioned above have a high potential to overlap acoustically with *P. mocinno* but the analysis revealed that they overlap little. This suggests some behavioural plasticity in the time pattern of their vocalisation leading to an acoustic avoidance. Nonetheless, conclusions regarding this particular case have to be taken with caution, and further analysis have to be conducted, as playback experiments testing the response of *P. mocinno* to the vocalizations of the four other species.

G. brasilianum, *C. occipitalis*, *H. cachinnans* and *H. leucophrys* had a low acoustic overlap with *P. mocinno*. The interaction of these species with *P. mocinno* in the community is probably low, and their respective ecological niches could be well differentiated.

The predator species, *M. ruficollis*, was the one that overlapped the less with the vocalizations of *P. mocinno* even if this predator species vocalizes quite similarly to *P. mocinno* (Fagan & Komar, 2016), and has a frequency bandwidth overlapping highly with *P. mocinno*. The low acoustic overlap could be another example of temporal interference avoidance (Planqué & Slabbekoorn, 2008). This acoustic avoidance could also be related to the predation pressure imposed by *M. ruficollis*. *P. mocinno* avoiding to vocalize when *M. ruficollis* does, to elude being localized by the predator.

Aulacorhynchus prasinus is a predator of *P. mocinno* and a fruit competitor. The species had a low acoustic overlap with territorial and alarm vocalizations of *P. mocinno*, as other predators in the acoustic community (*M. ruficollis* and *H. cachinnans*). *Aulacorhynchus prasinus* is dominant over *P. mocinno* and sometimes displace them from their perch (Santana & Milligan, 1984). Physical contact and intense chases have been observed between *P. mocinno* and *A. prasinus* (Wheelwright, 1983), the species is known to attack the chicks and eggs of *P. mocinno* (Skutch, 1967), and competes also for nest sites and fruits. Thus, *P. mocinno* probably avoid to vocalize when hearing *A. prasinus*, avoiding being noticed by this dominant species.

Despite that *P. mocinno* competes with *A. prasinus* for some of the same fruit species, the acoustic overlap was low, contrary to which was observed with other frugivorous species. The pressure imposed by the competition for food, might be surpassed by the dominance of *A. prasinus* over *P. mocinno*. The competition pressure for

food between *A. prasinus* and *P. mocinno* could be mitigated by a partition in space at foraging, caused by different methods to feed of each species, and differences in selectiveness. *Aulacorhynchus prasinus* use the method of hopping to take the fruits, reaching them from perch while *P. mocinno* use the sallying method (Santana & Milligan, 1984), taking the fruits in the air, and returning to the perch to feed (Avila et al., 1996). Before to sally, *P. mocinno* scan the surrounding area for fruits, and then generally takes only one fruit per flight. The energy obtained from that unique fruit must compensate the costs of flying for it. It is important for *P. mocinno* to recognize the quality of a fruit and be selective. *Aulacorhynchus prasinus* is less selective, taking as many fruits found, regardless their quality. Taking fruits in the air like *P. mocinno*, requires more space to fly, while *A. prasinus* requires branches for perching while eating, thus both species may use different areas in the same tree (Santana & Milligan, 1984). In addition *A. prasinus* does not make vertical migrations, and is not restricted to well preserved cloud forests, as *P. mocinno*. These differences in behaviour and ecology might reduce ecological competition between *P. mocinno* and *A. prasinus*, and could be related to the low acoustic overlap between them.

While vocalizations of *A. prasinus* had a low overlap with the territorial and alarm vocalizations of *P. mocinno*, they had a high overlap with the courtship vocalization. It is not clear the reason of this high overlap, but it could be due to a mutual interest of the area for the two species, nevertheless more studies are necessary to answer this question.

Migratory species, feeding on similar resources as *P. mocinno* can inflict pressure on the available food resources. The vocalizations of *Catharus ustulatus* overlapped the most with the alarm vocalizations of *P. mocinno*, and was the second overlapping the most with the territorial vocalizations after *T. mexicanus*. *Catharus ustulatus* is a migratory species, arriving to the forests of Guatemala for the non-breeding period of *P. mocinno*. It forages on the same canopy stratus than *P. mocinno* and feeds on insects, fruits and berries (Holmes & Robinson, 1988), probably some of the same plant species than *P. mocinno*. The vocalizations of *C. ustulatus* are repetitive and were the most abundant after *T. mexicanus*. Probably, they compete for food resources and feeding areas, stimulating the production of alarm vocalizations of *P. mocinno* when they concur on feeding sites. The quantity of migrant individuals arriving could vary between periods of migrations, and this could be revealed in the overlap rate observed.

In the present study, a detailed quantification of acoustic overlap in time and frequency has been made, and the strongest ecological niche competitors with *P. mocinno* have been identified. Competitors with *P. mocinno* have been reported in previous studies,

nevertheless this is the first quantification of the competition taking in consideration the acoustic resource. The results presented here can be useful as a base to conduct other specific studies in the community of *P. mocinno*. The analysis presented where done focused on *P. mocinno*, but similar analysis should be done for the competing species to have a better image of all interactions between all species. The same methodology can be applied in other communities and animal groups, in order to task important ecological problems.

4.6 Acknowledgements

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Chapter 5: General discussion



Couple of Resplendent Quetzals in Refugio del Quetzal reserve, San Marcos (Picture: Pablo Bolaños)

The general aim of this PhD was to investigate the acoustic behaviour and ecology of the Resplendent Quetzal by analysing its vocalizations in representative cloud forests in Guatemala.

This general discussion aims at summarizing the knowledge about the behaviour and population status of the Resplendent Quetzal, emphasizing the fields needing more attention. This thesis aims to contribute to the knowledge and conservation of this emblematic bird.

5.1 Vocal behaviour of the Resplendent Quetzal

Two subspecies of Resplendent Quetzals with no contact between them have been recognized: *P. m. mocinno* in the north part of its distribution, and *P. m. costaricensis* in the south part, separated by the lowlands of Nicaragua. Nevertheless, genetic and morphometric studies (Solórzano and Oyama 2009) suggested that they are two different species. This hypothesis was also supported by our acoustic analysis of territorial vocalizations (Chapter 1). The analysis revealed that *P. mocinno* produces vocalizations with higher frequency than *P. costaricensis*, while the first is larger in body size than the second. This result contradicts the general hypothesis that larger individuals have vocalizations lower in frequency than smaller ones (Fletcher 2004; Martin et al. 2011). The frequency difference could be due to an adaptation to different characteristics of the habitat between the northern distribution (*P. mocinno*) and the southern one (*P. costaricensis*) that leads to a modification of the frequencies according to the acoustic adaptation hypothesis (AAH). This hypothesis assumes that animal vocalizations have evolved so that their propagation in the habitat is maximized (Morton 1975; Wiley and Richards 1978). This could indicate that in the Costa Rican and Panamanian cloud forests, the vegetation is more dense than in the region of north Nicaragua to Chiapas and to counteract this density effect, *P. costaricensis* uses vocalizations that can travel further away, i.e. lower in frequency (Evans and Bazley 1956). Nevertheless, frequencies of *P. mocinno* vocalizations also could be tuned as well to avoid interference with vocalizations of other species in the community, as stipulated by the Acoustic Niche Hypothesis (ANH). In order to respond this question, a detailed comparison of the vegetal and animal diversity of the forests along the distribution of both subspecies still needs to be conducted. Other phenomena like genetic drift or sexual selection cumulated by years of separation also could explain the differences between vocalizations of both species.

Like other species in the family Trogonidae, *P. mocinno* vocalizations tend to be repetitive and acoustically monotonous in both sexes (Johnsgard 2000). Until now, vocalizations of the Resplendent Quetzal were not formally described, and available descriptions were onomatopoeic only (LaBastille, Allen, and Durrell 1972; Skutch 1944).

According to our observations of *P. mocinno* individuals during emission of vocalizations, four clear types were identified (Chapter 1), two for long range communication (territorial and alarm) and two for low range (courtship and contact). Logically the two long range vocalizations have been the most represented in sound libraries, the courtship vocalization being poorly represented and the contact vocalization being previously absent in public archives.

Vocalizations of *P. mocinno* seem to be well adapted to their habitat. According to propagation experiments (Chapter 1), the species produces vocalizations capable to travel long distances through the dense cloud forest. The vocalizations of *P. m. mocinno* cover a frequency range between 560 and 2860 Hz, which is relatively low compared to most of other bird species of tropical areas that produce vocalizations between 2000 to 3000 Hz (Catchpole and Slater 2008) but still falls into the Morton window (Morton 1975). The quantitative description made in Chapter 1, together with the propagation features in the cloud forest, support previous remarks on the vocal behaviour of the Resplendent Quetzal (LaBastille et al. 1972; Skutch 1944). The territorial vocalizations of *P. mocinno* are repetitive and stereotyped (Skutch 1944). Repetition of stereotyped sounds gives a better chance to be identified by a potential partner. In contrast, the short range courtship and contact signals produced by *P. mocinno*, are less repetitive and stereotyped, ensuring communication with conspecifics but avoiding the detection by predators.

Knowledge about the function of each vocalization type of *P. mocinno* is useful for monitoring purposes. Long range, stereotyped and repetitive vocalizations are ideal candidates for automatic detection systems. Quantification of vocalizations of various types also could be a valuable tool to identify territories or important areas for courtship or feeding.

A method using vocalizations to study *P. mocinno* individuals and population trends has several advantages. The population of *P. mocinno* is decreasing (Birdlife International 2016) and the number of individuals is not well determined. This lack of knowledge is partly due to a deficiency in the monitoring methods available. The Resplendent Quetzal is difficult to observe in its habitat and its high cultural importance imposes restrictions to study the species by invasive methods. Thus, non-invasive

methods like recording and analysis of vocalizations, has a high potential to study *P. mocinno* individuals and populations in its habitat.

5.2 Acoustic monitoring of *P. mocinno*

5.2.1 Population monitoring

The particular behaviour and relatively cryptic coloration of *P. mocinno*, makes it challenging to be studied and monitored using traditional methods like line transects or point counts. Direct observation in its habitat can be difficult due to the dense vegetation of the cloud forest and human presence can alter the behaviour of the species. In addition, owed to its rareness and high cultural importance, installing devices to track individuals could be controversial or non-ethical. Indeed, the setting up of electronic devices on the bird could affect its behaviour and increase predation risk and mortality (Mech and Barber 2002). Sometimes individuals maintain the devices installed even after a total battery loss (Powell and Bjork 1995) or after the study ends. In much of the study protocols, the de-installation of the monitoring device, is almost not possible due to the difficulty to catch the same individual twice (Paiz 1996; Powell and Bjork 1995; Yurrita 2013). Furthermore, these methods could be highly expensive and require the availability of trained biologists in the field.

Acoustic methods, non-invasive and less expensive, seem more reliable. In addition, autonomous recording equipment can be installed in the field and programed to work without human presence. Nevertheless, autonomous recording can generate a high amount of data that could be time consuming with manual methods of analysis. However, automatic detection methods can accelerate the analysis.

Automatic detection methods has been applied with success to study Neotropical birds (Ovaskainen, Moliterno de Camargo, and Somervuo 2018; Trifa et al. 2008; Ulloa et al. 2016), nevertheless, until now it has never been used to study the Resplendent Quetzal. The cross correlation method to detect automatically *P. mocinno* vocalizations presented in Chapter 3 appears effective in monitoring simultaneously several sites. The actual range of the automatic system to detect vocalizations was determined and the influence of weather conditions on the amount of vocalizations obtained was quantified. This method can be adapted to monitor *P. mocinno* populations in other forests.

It was determined that weather conditions can affect the number of automatic detections obtained (Chapter 3). Direct wind incidence inhibits the quantity of automatic

detections. This could be due to a masking effect of wind sound on *P. mocinno* vocalizations, but the possibility that the acoustic activity of *P. mocinno* is reduced by wind could be an alternative motive. Cloudiness is another weather factor affecting the number of automatic detections. It is known that *P. mocinno* is more active in cloudy and humid conditions (LaBastille et al. 1972) but this behaviour was not quantified before. This information is important to develop a correct interpretation of results in a monitoring protocol.

Propagation experiments to determine the active space of the automatic system used to detect *P. mocinno* vocalizations revealed a minimum active space between 16 m and 64 m, with a threshold for the cross correlation of 0.4. With lower thresholds, the active space is larger, but the number of false positive detections is also higher. Therefore, in a monitoring program of *P. mocinno* using the system presented here, recorders should be placed with a space of at least at 64 meters between them.

5.2.2 Adaptation of acoustic monitoring to different forests

The automatic detection system of *P. mocinno* vocalizations presented in Chapter 3 was tested in “Los Andes” reserve, a cloud forest located in the south slope of the Atitlan volcano in Guatemala. All bird monitoring methods, either manual or automatic, generate an error rate. In the case of the acoustic monitoring described in Chapter 3, the source of error was identified, being in most of cases vocalizations of other bird species.

An implementation of our automatic detection system in other forests can lead to different error rates due to other species not present in the first site. For example, a preliminary test of our automatic detection system was done in another protected area from Guatemala, “Sierra de las Minas”, and the results gave a high amount of false positive detections, caused by vocalizations of howler monkeys (*Alouatta pigra*). Howler monkeys produce loud vocalizations during male-male competitive interactions, which gives the vernacular name of the taxon (Kitchen et al. 2018). Their loud, low frequency roars overpass the bandwidth of *P. mocinno* vocalizations (Bergman et al. 2016), leading to a non-negligible amount of false positive detections. In order to solve this issue, we generated a specific template to detect *A. pigra* in order to avoid false positive detections of *P. mocinno* vocalizations. In Figure 1 is shown the number of detections of *P. mocinno* and *A. pigra*. The large amount of detections of *A. pigra* compared to *P. mocinno* vocalizations is evident. Thus, an adaptation of the system seems necessary to use it in these areas.

In summary, the automatic detection system developed here can be applied in other forests to monitor *P. mocinno* along its area of occurrence. In this case, it will be necessary to take into consideration some distinctive characteristics of the area studied, such as the presence of other species that can cause false positives.

5.2.3 Individual tracking

Bird vocalizations transmit efficient information regarding identity of the emitter (Aubin et al. 2004; Moseley and Wiley 2013; Odom, Slaght, and Gutiérrez 2013; Peake et al. 1998) and this can be useful to study behavior, mortality rates, or as a marking technique for capture-recapture protocols. Vocalizations have been used to differentiate individuals of the Mexican Antthrush (*Formicarius moniliger*) (Kirschel 2009). Vocal individuality has been applied to estimate movement patterns of the Corncrake (*Crex Crex*) (Peake and McGregor 2001) or to estimate the number of calling males of Scops Owls (*Otus scops*) (Denac and Trilar 2006). Nevertheless, to use vocalizations as a marking method of individuals, it is necessary to validate some assumptions.

Stability of vocalizations have to be assumed in an acoustic marking method, ensuring that vocalizations does not change between years (Terry, Peake, and McGregor 2005). Non learning vocal species are therefore more suitable for detection of acoustic individuality. *P. mocinno* is a non-passerine bird that, a priori, does not learn its vocalizations but this assumption needs to be verified. Consequently, the first step is to measure the amount of natural variation among individuals. Thus, it is necessary to have recordings where the identity of the emitter is known. This supposes to identify birds by another method, ringing for example, or to record vocalizations of individuals with an absolute confidence about the emitter, maybe based on their recording location and song timing (Kirschel et al. 2009). After this step solved, vocal detection of individuals would have a high potential to be included in studies of *P. mocinno* with direct implications for the species conservation.

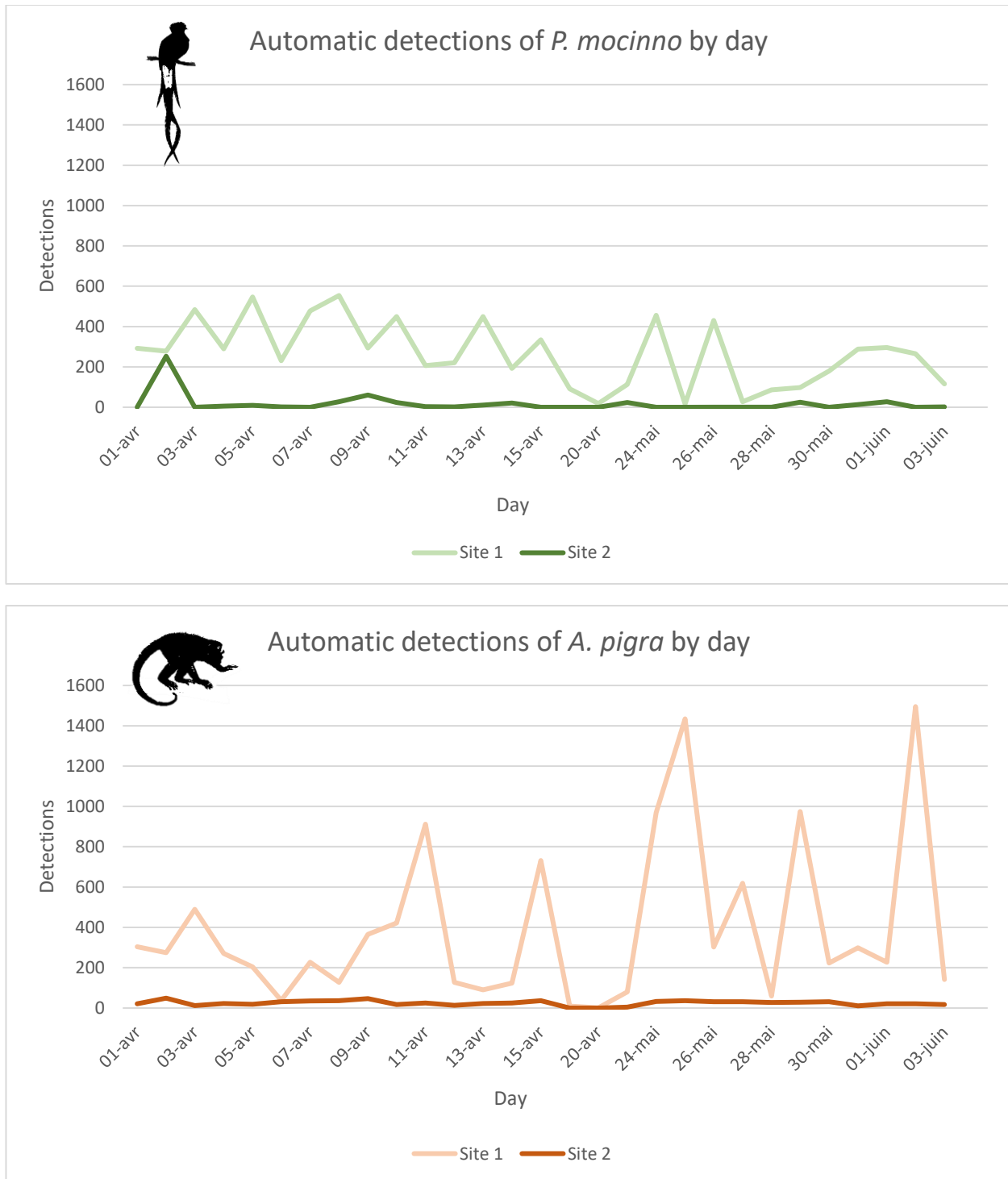


Figure 63: Dynamics of vocal activity of *P. mocinno* and *A. pigra*, detected in Sierra de las Minas by cross correlation. Data obtained in two sites on April – May 2018. Data provided by Defensores de la Naturaleza Foundation, and Renace (CMI), Guatemala

5.3 Habitat conservation of the Resplendent Quetzal

To protect Resplendent Quetzal populations, it is necessary to protect their habitat. The species is restricted to the cloud forest, along the year individuals move from their nest sites in elevated portions of the mountains to sites located in lower parts. Cloud forest habitat requires several features to be maintained, the most important being a high relative humidity, moderate temperatures and high elevations (Ataroff and Rada 2000; Holder 2004). Particular areas of mountains and volcanoes of the intertropical zone usually offer these weather characteristics, so that cloud forest most often occupies the slopes of these landscapes. The two main principal threats acting on the cloud forest habitat are deforestation (Pope and Harbor 2014) and climate change (Chape, Spalding, and Jenkins 2008).

5.3.1 Habitat fragmentation and connectivity between forests

The most vulnerable areas to deforestation are the lower parts of volcanoes and mountains, due to a low inclination favouring accessibility and, hence, the establishment of agriculture fields (Pope and Harbor 2014). Such selective deforestation induces a fragmentation of the cloud forest (Solorzano, Garcia-Juarez, and Oyama 2009), possibly affecting the vertical migration of the Resplendent Quetzal from the high to the low parts of landscape (Powell and Bjork 1995). Fragmentation reduces, or even interrupts, connections and gene flow between distant populations. Some forests have been highly isolated, losing connectivity between them (Solorzano et al. 2009). Ecological connectivity can be explained as the capacity of a landscape to allow movements of species and populations within habitat remnants with resources (Taylor et al. 1993). Maintaining connections among forests is a necessary constituent of a reserve system. Species with populations distributed through different landscape fragments have to move across the patches for maintaining genetic variability. The capacity to move from one patch to another is different for each species (Groom, Meffe, and Carroll 2006). *Pharomachrus mocinno* is not characterized by a high capacity to fly long distances. Seasonal migration of *P. mocinno* between different forest fragments could have important implications for its long term conservation since the interchange of individuals within different populations maintains the genetic variability and consequently ensures a greater viability of wild populations (Paiz 1996; Powell and Bjork 1995).

Some fragments of the remnant cloud forest are considered to be smaller than the size necessary to maintain viable *P. mocinno* populations (Renner 2003). Mühlenberg et

al. (1989) suggested that a minimal density for *P. mocinno* is 33 males/ km², and the minimum area to maintain viable meta-populations with no presumed exchange of individuals is 50.5 km². In a study of connectivity in the region named “Corredor del Bosque Nuboso” located in north east of Baja Verapaz department in Guatemala and covering an area of 199.9 km² (Yurrita 2013), the landscape is composed of 105 fragments, among these, 58 have less than 0.87 km², eight have an area between 1.04 and 6.57 km², and just three fragments are superior to 23.8 km². One of these is the forest of Sierra de las Minas which is the largest cloud forest in Guatemala, with 47.1 km², the other two fragments are the natural reserves “Biotopo Universitario para la Conservación del Quetzal Mario Dary Rivera”, and “Cerro Verde”. Yurrita *et al.* (2013) considered as the minimum area (2.5 km²) to maintain at least one reproductive pair. Small fragments connecting large forests are important to maintain *P. mocinno* populations. Apart of connecting larger forests, these small areas are important for the feeding of *P. mocinno* on the seasonal migration during the non-breeding period (Powell and Bjork 1995).

Telemetry studies have evidenced the occurrence of seasonal movements between forests in “Sierra de las Minas” and “Sierra de Chuacús” (Paiz 1996; Yurrita 2013). Genetic studies suggested that there are two genetic groups along the distribution of *P. m. mocinno*, one cluster in the south of Mexico, and another cluster in Guatemala, Nicaragua and El Salvador (Solorzano *et al.* 2009). In order to ensure the continuity of the genetic interchange between metapopulations of clusters, connectivity between patches is necessary. Thus, conservation programs including the maintenance of ecological connectivity is necessary to enhance the possibilities for the conservation of the genetic diversity of *P. mocinno* (Solorzano *et al.* 2009).

The acoustic monitoring system that we have developed (Chapter 3) could be used to track vertical migrations of *P. mocinno* in relation with the reduction of the forest at low elevations.

The same system could be then used to estimate the connections between the populations and the structure of the metapopulation. This information could be used to design species corridors, establishment of new protected areas or management of existing ones.

5.3.2 Climate change

An important characteristic of the cloud forest is the interception of moisture of clouds as they pass through the forest. A large proportion of water income (9%) are obtained by direct interception of clouds by leafs of forest canopy (Ataroff and Rada

2000). Climate change may interfere in factors as rain cycle patterns and temperatures (Sekercioglu, Primack, and Wormworth 2012). With warming, cloud forests capture less water and become drier (Karmalkar, Bradley, and Diaz 2008). Thus a reduction of cloudiness due to climatic change might impact the habitat (Chape et al. 2008). Cloudiness and humidity also can be reduced as deforestation increases (Holder 2004).

Behaviour of *P. mocinno* is related to cloudiness, the species vocalizing more actively when the cloud cover is greater (Chapter 2). Fluctuations in cloudiness can therefore influence the activity patterns of *P. mocinno*, if not its presence (Chapter 3). The iridescent colour of Resplendent Quetzal feathers makes the bird conspicuous when sunlight incidence is high. Nevertheless, when the weather is cloudy and humid, its plumage can be mistaken with the green surrounding of its habitat and the bird becomes less visible (LaBastille et al. 1972; Monge-Najera and Hernandez 1994). By this way, changes in usual cloudiness patterns can affect *P. mocinno* behaviour. The acoustic monitoring system could reveal the effect of cloudiness on the acoustic activity patterns of the Resplendent Quetzal suggesting that following the vocal activity of the Resplendent Quetzal could be a valuable tool to study peculiar effects of climatic change.

Areas affected by climate change are located in high latitude regions, but also in tropical areas at high elevations (Williams, Jackson, and Kutzbach 2007). Global warming has caused rapid shifts in populations of Neotropical bird species, affecting their distribution in montane species (Freeman and Class 2013). Bird species, occurring in elevated areas have a much smaller area of occupancy at the top of the mountain compared to its base (Sekercioglu et al. 2012). Changes in the structure of bird communities due to climate change may induce responses caused by pressures faced to a limited resource. In Chapter 4, the vocal response of *P. mocinno* challenged by a regular migrant species is discussed. Vocalizations of the migrant species *C. ustulatus* highly overlapped with the alarm and territorial vocalizations of *P. mocinno*, possibly triggered by competition for same fruit resources. Changes in migration patterns caused by climate change implicate a change in community structure. Special attention of the effects of climate change on bird communities have to be taken in consideration. Acoustics can be used as a tool to follow responses of species of a community to climate change, looking for interspecific acoustic interactions.

5.4 Patterns of ecological competition in the community of *P. mocinno*

Tackling questions regarding the processes influencing the structure of an ecological community can help to know how to manage and protect natural areas. The species composition of an ecological community is influenced by different processes, acting on different time scales. Abundance of individuals is determined by immigration, emigration, reproduction and mortality. On a short time scale (from hours to years), ecological interactions can reject or enable species in the community (Morin 2011). In the case *P. mocinno* population, the availability of fruiting trees and nest caves would be the major constraints influencing the relative abundance in the community (LaBastille et al. 1972). Therefore, the availability of these resources for *P. mocinno* highly depends as well on the use by other species in the community. Food, nest trunks, and acoustic resource, could be three major features structuring the community of *P. mocinno*. The Figure 64 shows the processes that take place in the community and that affect the species abundances and structure.

Interspecific interactions between *P. mocinno* and other species having a potential acoustic overlap in time and frequency with *P. mocinno* were evaluated in Chapter 4. Multifactorial analysis including acoustic overlap and other ecological features of competition, as nest types and food resources, revealed important patterns. Among the species included in the analysis, some had a high potential to overlap acoustically with *P. mocinno*. By measuring the difference between the potential acoustic overlap and the observed one, it was possible to know if an acoustic avoidance process exists as stipulated by the ANH. Multivariate analysis of acoustic overlap, together with other factors of competition between species, revealed the following general patterns:

- 1 Full or partially frugivorous bird species had a high observed acoustic overlap with *P. mocinno*.
- 2 Phylogenetically close species with *P. mocinno* had a high observed acoustic overlap.
- 3 Phylogenetically distant species with *P. mocinno* had a low observed acoustic overlap.
- 4 Predator species had a low observed acoustic overlap with *P. mocinno*.

- 5 Predator species (*A. prasinus*) also competing for fruit and nest type with *P. mocinno* had a low acoustic overlap with territorial and alarm vocalizations, but a high overlap with the courtship vocalization.
- 6 The only migratory species in the community (*C. ustulatus*) overlapped acoustically with the alarm and territorial vocalizations of *P. mocinno*.

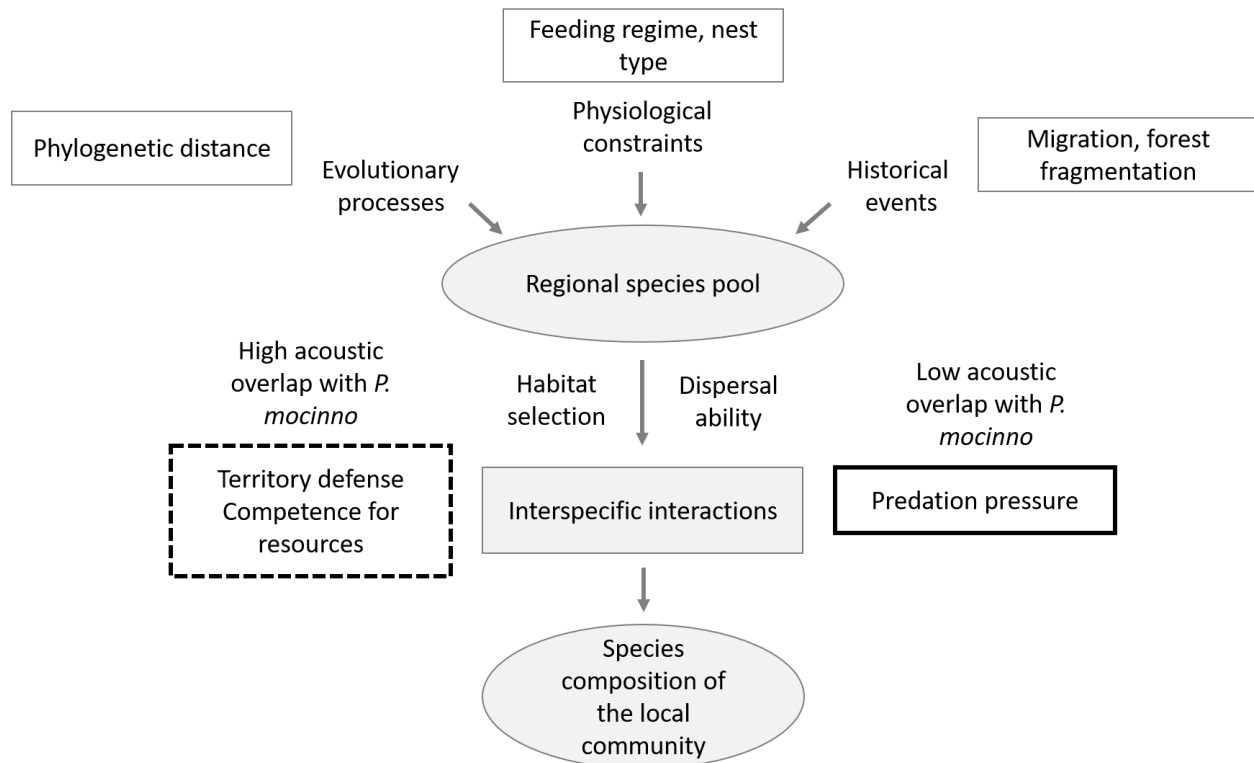


Figure 64: Species composition in a community is a product of a sequence of several factors interacting at a hierarchical way. Interspecific interactions can reduce or enhance inclusion of species in the community. Green square represents interaction enhancing vocal production, orange square interaction inhibiting vocal production in *P. mocinno* (diagram adapted from Morin 2011)

These patterns suggest that species in the community of *P. mocinno* may adapt on the short-term the rate of their vocalization so that interspecific acoustic overlap is reduced. This represents a type of interspecific interaction. The highest acoustic overlap with *P. mocinno* observed was with species competing directly for a shared resource and the lowest observed overlap, was with predator species (Figure 57, Figure 58 and Figure

59). A summary diagram of competition for resources with *P. mocinno* and how it affects acoustic overlap is provided in Figure 65.

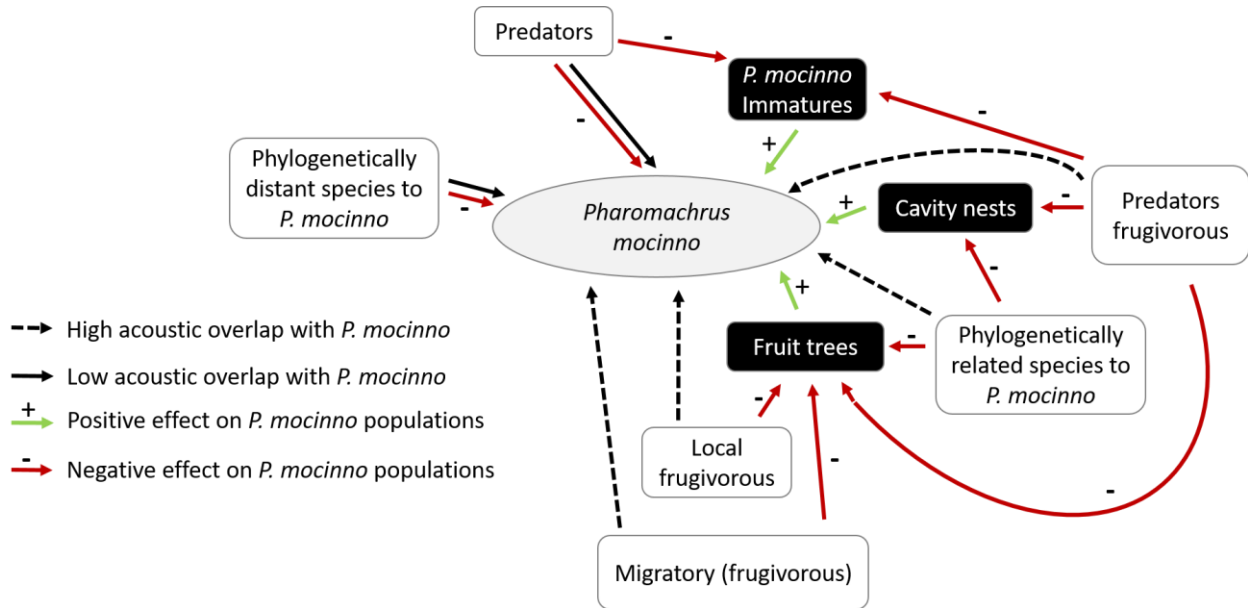


Figure 65: General scheme of competition in the acoustic community of *P. mocinno*. Specific circumstances may apply. Black squares represent positive resources for *P. mocinno*, red arrows are negative pressures and green arrows are positive pressures

Species phylogenetically close to *P. mocinno* have similar specializations on feeding and nest sites resource use. Therefore, *P. mocinno* and related species impose resource limits to each other. *Trogon mexicanus*, which belongs to the same family as *P. mocinno*, Trogonidae, was the species that overlap the most with the territorial vocalizations of *P. mocinno*.

Migratory species, feeding on similar resources as *P. mocinno*, probably inflict pressure on the available food resources. *Catharus ustulatus* was the species that overlapped the most with the alarm vocalizations of *P. mocinno*, and the second with the highest overlap with the territorial vocalizations, after *T. mexicanus*. The quantity of arriving migratory individuals of a given species, could vary from one year to the next, and this could be revealed in the overlap rate observed, reflecting competition between species.

Potential predator species of *P. mocinno* (especially *M. ruficollis*) had a low overlap with their vocalizations. The Resplendent Quetzal might avoid to vocalize when a predator vocalizes, so not to be detected by the predator.

A special case was observed with a predator species that also competes with *P. mocinno* for food and nest sites. Previous studies have suggested that the Emerald Toucanet (*A. prasinus*) is a strong competitor with the Resplendent Quetzal, and is also a predator of their eggs and chicks (Skutch 1967; Wheelwright 1983). The specialized methods of *P. mocinno* and *A. prasinus* to take fruits suggest that they could generally use different sites in the trees to feed, Resplendent Quetzal feeding in flight while Emerald Toucanets feeds perched. *A. prasinus* had a low overlap with territorial and alarm vocalizations of *P. mocinno*, nevertheless the first overlapped highly with the courtship vocalization of the second. This could indicate a kind of interaction between both species, related to breeding sites.

The new methodology to study of vocal communities exposed in Chapter 4 of this PhD thesis can be applied to tackle important questions regarding animal communities.

5.5 General conclusions

Through this PhD thesis, new methodologies have been proposed new methodologies to study animal species and diversity and particularly a first description of *P. mocinno* vocalizations, the development of an automatic acoustic monitoring system for the species and the proposal of a new methodology to study animal acoustic communities has been presented.

Tracking of *P. mocinno* populations could be used as a way to understand effects of the climate change.

The methodologies exposed can be applied to different places, or adapted to different species and vocal communities. The methodology proposed to study animal communities can be applied to test how acoustic indices could be related to biodiversity in a community. Furthermore, other important questions, for instance, the effect of invasive species, could be tackled by the use of the methodology exposed here to study communities.

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Chapter 6: Appendix

Appendix Chapter 2

Table S1: List and metadata of recordings collected in the field and in public archives. *Pmm*: *P. m. mocinno*, *Pmc*: *P. m. costaricensis*, *Pan*: *P. antisianus*, *Pau*: *P. auriceps*, *Pf*: *P. fulgidus*, *Pp*: *P. pavoninus*. BISAM: Biblioteca de Sonidos de Aves de México, UCR: Laboratorio de Bioacústica de la Universidad de Costa Rica

Recording	Location	Country	Latitude	Longitude	Author	Species	Library
33730_44k	Serrania Bellavista	Bolivia	N -15°39'	W -67°3'	T. Parker	<i>Pan</i>	Macaulay
13230_44k	San Martin	Peru	N -5°43.8'	W -77°31.2'	T. Parker	<i>Pan</i>	Macaulay
17779_44k	Huanuco	Peru	N -9°10.2'	W -75°28.8'	V. Emanuel	<i>Pan</i>	Macaulay
17869_44k	Huanuco	Peru	N -9°10.2'	W -75°28.8'	V. Emanuel	<i>Pan</i>	Macaulay
31879_44k	Huanuco	Peru	N -9° 10.19'	W -75° 28' 48"	T. Parker	<i>Pan</i>	Macaulay
17615_44k	Bosque Aputinaye	Peru	N -9° 10.19'	W -75° 28' 48"	T. Parker	<i>Pan</i>	Macaulay
13211_44k	San Martin	Peru	N -5° 43.8'	W -77° 31.19'	T. Parker	<i>Pan</i>	Macaulay
168735_44k	Los Cedros	Ecuador	N 0°19.318092'	W -78°47.22'	S. Olmstead	<i>Pau</i>	Macaulay
74696_44k	SW of Cosanga, Juan	Ecuador	N 0°40.999998'	W -77°55'	M. Robbins	<i>Pau</i>	Macaulay
139093_44k	Mindo	Ecuador	N 0° 1.77'	W -78° 44.59098'	M. Linda	<i>Pau</i>	Macaulay
147204_44k	Napo	Peru	N -11°28.32'	W -74°47.46'	M. Robbins	<i>Pau</i>	Macaulay
174014_44k	Cuzco	Peru	N -13°22.56'	W -73°8.22'	M. Robbins	<i>Pau</i>	Macaulay
147200_44k	Calabazas	Peru	N -11° 28.31'	W -74° 47.45999'	M. Robbins	<i>Pau</i>	Macaulay
XC102638	El Dorado	Colombia	N 11° 6.4679'	W -74° 2.92199'	F. Schmitt	<i>Pf</i>	Xeno-Canto
2007_02_03_A_503-514	Sierra Nevada Santa Marta	Colombia	N 11°06'	W 74°04'W	N. Krabbe	<i>Pf</i>	Personal
2007_02_13_B_187-189	Sierra Nevada Santa Marta	Colombia	N 11°06'	W 74°04'	N. Krabbe	<i>Pf</i>	Personal
XC227645_b17a	Rancho Grande	Venezuela	N 10° 20.3999'	W -67° 42'	P. Boesman	<i>Pf</i>	Xeno-Canto
32269_44k	Monteverde	Costa Rica	N 10°18.83382'	W -84°47.68746'	T. Parker	<i>Pmc</i>	Macaulay
39195_44k	Monteverde	Costa Rica	N 10°17.13708'	W -84°47.77014'	T. Parker	<i>Pmc</i>	Macaulay
39209_44k	Monteverde	Costa Rica	N 10°21.9003'	W -84°47.682'	T. Parker	<i>Pmc</i>	Macaulay
53907_44k	Monteverde	Costa Rica	N 10°15.99402'	W -84°49.26228'	D. Ross	<i>Pmc</i>	Macaulay

Recording	Location	Country	Latitude	Longitude	Author	Species	Library
72803_44k	Monteverde	Costa Rica	N 10°15.99402'	W -84°49.26228'	D. Ross	<i>Pmc</i>	Macaulay
72825_44k	Monteverde	Costa Rica	N 10°15.99402'	W -84°49.26228'	D. Ross	<i>Pmc</i>	Macaulay
76717_44k	Monteverde	Costa Rica	N 10°15.99402'	W -84°49.26228'	C. Marantz	<i>Pmc</i>	Macaulay
BLB20205	Villa Mills	Costa Rica	N 9°34.002'	W -83°40.998'	L. Baptista	<i>Pmc</i>	Macaulay
BLB20206	Villa Mills	Costa Rica	N 9°34.002'	W -83°40.998'	L. Sandra & L. Gaunt	<i>Pmc</i>	Macaulay
LBUCR000060	Carretera Interam. Km 60	Costa Rica	N 9°32.4'	W -83°54'	J. Sánchez	<i>Pmc</i>	UCR
XC137766	Monteverde	Costa Rica	N 10°18.3'	W -84°47.4'	P. Driver	<i>Pmc</i>	Xeno-Canto
XC274217	Cerro de la Muerte	Costa Rica	N 9°32.4'	W -83°54'	P. Boesman	<i>Pmc</i>	Xeno-Canto
6192_44k	Cerra Punta	Panama	N 8°50.172'	W -82°32.592'	E. Morton	<i>Pmc</i>	Xeno-Canto
XC271505	Cerro Punta	Panama	N 8°50.93208'	W -82°32.50758'	P. Boesman	<i>Pmc</i>	Xeno-Canto
XC271506	Cerro Punta	Panama	N 8°50.93208'	W -82°32.50758'	P. Boesman	<i>Pmc</i>	Xeno-Canto
0919.wav	Sierra de las Minas	Guatemala	N 15°9.33228'	W -89°38.56476'	A. Martínez	<i>Pmm</i>	Personal
137688_44k.wav	Los Trrales	Guatemala	N 14°33.6'	W -91°10.08'	M. Medler	<i>Pmm</i>	Macaulay
137692_44k.wav	Los Trrales	Guatemala	N 14°33.6'	W -91°10.08'	M. Medler	<i>Pmm</i>	Macaulay
160211-010.wav	Los Andes	Guatemala	N 14°32.9268'	W -91°11.00226'	P. Bolaños-Sittler	<i>Pmm</i>	Personal
170326_0567	Refugio del Quet. S. Marcos	Guatemala	N 14°56.571'	W -91°52.28202'	P. Bolaños-Sittler	<i>Pmm</i>	Personal
172695_44k	Los Trrales	Guatemala	N 14°33.348'	W -91°9.9876'	J. de León	<i>Pmm</i>	Macaulay
6193_44k.wav	E Lake and Volcano Atitlan	Guatemala	N 14°35.07348'	W -90°10.74522'	A. LaBastille	<i>Pmm</i>	Macaulay
130609-12	Ranchitos del Quetzal	Guatemala	N 15°12.92934'	W -90°13.15494'	P. Bolaños-Sittler	<i>Pmm</i>	Personal
170120_0555	Refugio del Quet. S. Marcos	Guatemala	N 14°56.43798'	W -91°52.35198'	P. Bolaños-Sittler	<i>Pmm</i>	Personal
160211-013	Los Andes	Guatemala	N 14°32.77602'	W -91°11.118'	P. Bolaños-Sittler	<i>Pmm</i>	Personal
160211-011	Los Andes	Guatemala	N 14°32.77602'	W -91°11.118'	P. Bolaños-Sittler	<i>Pmm</i>	Personal
170907-003	Ranchitos del Quetzal	Guatemala	N 15°12.92934'	W -90°13.15494'	P. Bolaños-Sittler	<i>Pmm</i>	Personal
XC108437	Cusuco	Honduras	N 15°33.12'	W -88°17.76'	S. Jones	<i>Pmm</i>	Xeno-Canto
120315_08.wav	El Triunfo, Chiapas	Mexico	N 15°40.00554'	W -92°48.0021'	F. González-García	<i>Pmm</i>	BISAM
120418_02.wav	El Triunfo, Chiapas	Mexico	N 15°40.00554'	W -92°48.0021'	F. González-García	<i>Pmm</i>	BISAM
127213_44k.wav	El Triunfo, Chiapas	Mexico	N 15°39.53333'	W -92°48.7'	C. Marantz	<i>Pmm</i>	Macaulay
130417_00.wav	El Triunfo, Chiapas	Mexico	N 15°40.00554'	W -92°48.0021'	F. González-García	<i>Pmm</i>	BISAM

Recording	Location	Country	Latitude	Longitude	Author	Species	Library
140220_15.wav	El Triunfo, Chiapas	Mexico	N 15°40.00554'	W -92°48.0021'	F. González-García	<i>Pmm</i>	BISAM
140221_0051.wav	El Triunfo, Chiapas	Mexico	N 15°40.00554'	W -92°48.0021'	F. González-García	<i>Pmm</i>	BISAM
140221_0054.wav	El Triunfo, Chiapas	Mexico	N 15°40.00554'	W -92°48.0021'	F. González-García	<i>Pmm</i>	BISAM
140221_0055.wav	El Triunfo, Chiapas	Mexico	N 15°40.00554'	W -92°48.0021'	F. González-García	<i>Pmm</i>	BISAM
140318_76.wav	El Triunfo, Chiapas	Mexico	N 15°40.00554'	W -92°48.0021'	F. González-García	<i>Pmm</i>	BISAM
140319_0034.wav	El Triunfo, Chiapas	Mexico	N 15°40.00554'	W -92°48.0021'	F. González-García	<i>Pmm</i>	BISAM
140320_0077.wav	El Triunfo, Chiapas	Mexico	N 15°40.00554'	W -92°48.0021'	F. González-García	<i>Pmm</i>	BISAM
6189_44k.wav	Comitan, Chiapas	Mexico	N 16°57.702'	W -91°57.5611'	A. May	<i>Pmm</i>	Macaulay
86687_44k.wav	El Triunfo, Chiapas	Mexico	N 15°39'	W -92°49.002'	C. Duncan	<i>Pmm</i>	Macaulay
86650_44k	N of Emiliano Zapata	México	N 17°10'	W -92°25'	C. Duncan	<i>Pmm</i>	Macaulay
95076_44k	El Triunfo, Chiapas	México	N 15°39'	W -92°49'	C. Hanks, & B. O'Shea	<i>Pmm</i>	Macaulay
64749.wav	West of Ariqueemes, Rondonia	Brazil	N 9°-53.916'	W -63°16.084'	K. Zimmer	<i>Pp</i>	Macaulay
37386_44k	North of Rio Maniti, Loreto	Peru	N -3°27'	W -72°51'	M. Robbins	<i>Pp</i>	Macaulay
37506_44k	Rio Maniti, Loreto	Peru	N -3°27'	W -72°51'	M. Robbins	<i>Pp</i>	Macaulay
76091_44k	Madre de Dios	Peru	N -12°49.002'	W -69°24'	C. Marantz	<i>Pp</i>	Macaulay

Acoustic behavior and ecology of the Resplendent Quetzal *Pharomachrus mocinno*, a flagship tropical bird species

The Resplendent Quetzal *Pharomachrus mocinno* is a tropical bird considered in a high risk of danger. Degradation of its habitat caused by human activities is the principal menace. The Resplendent Quetzal is important as seed disperser and is the centre of the past and present Mayan culture. The available studies about the species have covered aspects of the natural history and biology. Nevertheless, the description of the acoustic behaviour and ecology, a prerequisite for the conservation of the species, was not available. The general aim of this PhD thesis was to investigate the acoustic behaviour and ecology of *P. mocinno* in the cloud forest of Guatemala. A detailed analysis of *P. mocinno* vocalizations, including propagation experiments of these vocalizations in its habitat, led to identify two vocalizations intended for long range, and two for short range communication. Quantification of acoustic parameters in territorial vocalizations of the two subspecies of the Resplendent Quetzal, *P. m. mocinno* (north part of Central America and Chiapas) and *P. m. costaricensis* (south part of Central America), revealed clear differences between the subspecies, that could support a species separation hypothesis. The observation of the species in the dense canopy is difficult and manipulation of individuals is controversial due to its high cultural importance. Then, an automatic acoustic system was developed as a method to study the species in a non-invasive way. The system proved to be efficient and returned results that revealed acoustic patterns linked to environmental variables. Finally, the acoustic community of other bird species *P. mocinno* belongs to was analysed so that interspecific competition interactions could be assessed. The research here developed should help in future conservation decisions about the Resplendent Quetzal and its habitat, the cloud forest. This research also illustrates that ecoacoustics can be a valuable strategy to tackle ecology and conservation questions in tropical areas.

Keywords: bioacoustics – bird vocalizations – *Pharomachrus mocinno* – Resplendent Quetzal – Trogonidae – acoustic community – acoustic monitoring

Comportement et écologie acoustiques du Quetzal Resplendissant *Pharomachrus mocinno*, une espèce porte drapeau d'oiseau tropical

Le Quetzal Resplendissant *Pharomachrus mocinno* est une espèce d'oiseau tropical considérée fortement menacée par la perte de son habitat due aux activités humaines. Le Quetzal Resplendissant joue un rôle important de disperseur de graines et constitue le centre de la culture maya passée et présente. Les recherches sur cette espèce couvrent plusieurs aspects de son histoire naturelle et de sa biologie. Néanmoins, à ce jour, il n'y a aucune description détaillée du comportement et de l'écologie acoustiques de cette espèce, condition préalable à une conservation efficace de l'espèce. L'objectif de cette thèse a été d'étudier tout particulièrement le comportement et l'écologie acoustique de *P. mocinno* dans la forêt nuageuse du Guatemala. Une analyse détaillée des vocalisations de *P. mocinno*, incluant des expériences de propagation de ses vocalisations dans son habitat, a permis d'identifier deux types de vocalisations destinés à la communication à longue distance et deux autres types de vocalisations destinés à la communication à courte distance. La quantification des différences dans les vocalisations territoriales des deux sous-espèces de Quetzals Resplendissants, *P. m. mocinno* (partie nord de l'Amérique centrale et sud du Mexique) et *P. m. costaricensis* (sud de l'Amérique centrale) a révélé de nettes différences entre les sous-espèces, ce qui conforterait l'hypothèse d'espèces distinctes. L'observation de l'espèce dans la canopée dense est difficile et la manipulation des individus est controversée en raison de sa grande importance culturelle. De fait, un système acoustique automatique a été mis au point pour suivre l'espèce de manière non invasive. Le système s'est avéré efficace et a produit des résultats révélant des profils de suivis acoustiques en partie dépendants de variables environnementales. Enfin, la communauté acoustique des oiseaux à laquelle *P. mocinno* appartient a été analysée afin d'évaluer les interactions interspécifiques de compétition. Les recherches développées ici devraient aider aux décisions de conservation futures concernant le Quetzal Resplendissant et son habitat, la forêt nuageuse. Cette recherche montre également que l'écoacoustique peut constituer une stratégie utile pour aborder les problèmes d'écologie et de conservation dans les zones tropicales.

Mots clés : bioacoustique – vocalisations des oiseaux – *Pharomachrus mocinno* – Quetzal Resplendissant – Trogonidae – communauté acoustique – suivi acoustique

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