UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE BIOLOGÍA
ECOLOGÍA

REQUERIMIENTOS ECOLÓGICOS DEL LORO CORONA AZUL (*Amazona guatemalae*) EN LA REGIÓN DE LOS CHIMALAPAS, OAXACA, MÉXICO

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

MIGUEL ÁNGEL DE LABRA HERNÁNDEZ

TUTORA PRINCIPAL DE TESIS: DRA. KATHERINE RENTON
INSTITUTO DE BIOLOGÍA, UNAM
COMITÉ TUTOR: DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA
FACULTAD DE ESTUDIOS SUPERIORES IZTACALA, UNAM
DRA. BERTHA PATRICIA ESCALANTE PLIEGO
INSTITUTO DE BIOLOGÍA, UNAM

MÉXICO, CD. MX. DICIEMBRE, 2016.

UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE BIOLOGÍA
ECOLOGÍA

REQUERIMIENTOS ECOLÓGICOS DEL LORO CORONA AZUL (*Amazona guatemalae*) EN LA REGIÓN DE LOS CHIMALAPAS, OAXACA, MÉXICO

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

MIGUEL ÁNGEL DE LABRA HERNÁNDEZ

TUTORA PRINCIPAL DE TESIS: DRA. KATHERINE RENTON
INSTITUTO DE BIOLOGÍA, UNAM
COMITÉ TUTOR: DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA
FACULTAD DE ESTUDIOS SUPERIORES IZTACALA, UNAM
DRA. BERTHA PATRICIA ESCALANTE PLIEGO
INSTITUTO DE BIOLOGÍA, UNAM

MÉXICO, CD. MX. DICIEMBRE, 2016.

UNAM
POSGRADO
Ciencias Biológicas

COORDINACIÓN

Lic. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión del Subcomité por Campo de Conocimiento de Ecología y Manejo Integral de Ecosistemas del Posgrado en Ciencias Biológicas, celebrada el día 5 de septiembre de 2016, se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del alumno **DE LABRA HERNÁNDEZ MIGUEL ANGEL** con número de cuenta **513014765** con la tesis titulada: **"Requerimientos ecológicos del loro corona azul (*Amazona guatemalae*) en la región de los Chimalapas, Oaxaca, México"**, realizada bajo la dirección de la **DRA. KATHERINE RENTON:**

Presidente:	DR. ADOLFO GERARDO NAVARRO SIGUENZA
Vocal:	DR. IAN MACGREGOR FORS
Secretario:	DRA. MARIA DEL CORO ARIZMENDI ARRIAGA
Suplente:	DR. ALEJANDRO SALINAS MELGOZA
Suplente	DRA. ROSA IRMA TREJO VAZQUEZ

Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARA EL ESPIRITU"
Cd. Universitaria, Cd. Mx, a 4 de noviembre de 2016.

M. del Coro Arizmendi

DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA
COORDINADORA DEL PROGRAMA

c.c.p. Expediente del (la) interesado (a).

AGRADECIMIENTOS

Al Posgrado en Ciencias Biológicas de la Universidad Nacional Autónoma de México, particularmente al personal administrativo.

Al Consejo Nacional de Ciencia y Tecnología (CONACyT) por la beca No. 215549 que me permitió realizar mis estudios de Doctorado.

Al Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (UNAM-DGAPA-PAPIT-IN205716), otorgado a la Dra. Katherine Renton.

A la Secretaría de Medio Ambiente y Recursos Naturales quienes otorgaron los permisos para la investigación.

A mi tutora, la Dra. Katherine Renton por su apoyo académico, dirección y enseñanzas, claves en el desarrollo de mi proyecto de investigación y formación académica.

A los miembros de mi Comité tutor: Dra. María del Coro Arizmendi Arriaga y Dra. Bertha Patricia Escalante Pliego por sus acertadas observaciones a lo largo del proceso.

AGRADECIMIENTOS A TÍTULO PERSONAL

A mis padres, María del Carmen Hernández Pérez y Vicente Delabra Benítez, y hermanos Mirthe, Saúl y Bere, por su infinito amor, confianza, apoyo y porque siempre han creído en mí.

A toda mi familia, porque los momentos juntos son hermosos. En especial a mis hermosas abuelitas Rufina Pérez y Aurora Benítez, por sus enseñanzas de vida, consejos y miles de oraciones. A la memoria de mis abuelitos Francisco Hernández y José Delabra.

A Kathy, por "adoptarme" como estudiante (pollo) y enseñarme como se debe hacer investigación. Gracias por asesorarme, guiarme y corregirme cada vez que no hacía bien las cosas. Finalmente por el enorme ser humano que eres, Kathy muchas gracias.

A Marisela por su amor y amistad incondicional, por siempre estar a mi lado en las buenas y en las malas, eres mi compañera de vida.

A mi Comité tutor: Dra. María del Coro Arizmendi Arriaga y Dra. Bertha Patricia Escalante Pliego por todos sus comentarios y correcciones que a lo largo del tiempo se ven reflejados en este trabajo.

A mi jurado de Tesis: Dr. Adolfo Gerardo Navarro Sigüenza, Dr. Ian MacGregor Fors, Dra. María del Coro Arizmendi Arriaga, Dr. Alejandro Salinas Melgoza, y Dra. Rosa Irma Trejo Vázquez, por sus críticas y acertadas observaciones que mejoraron este trabajo de Tesis.

A José María Martínez y María Guadalupe Ruíz por su apoyo y convivencia familiar.

A Alejandro Salinas, por sus pláticas, ideas y ser accesible cuando pedí correcciones en el artículo de investigación.

A Maris, Gladys y Alex Salinas por su compañía en campo.

A Rocío Gonzáles Acosta por su paciencia y ayuda en todos los trámites durante el posgrado.

Por último quiero agradecer a las autoridades de Bienes Comunales del municipio de Santa María Chimalapa, por el permiso brindado para la realización del trabajo de campo en las comunidades de Chalchijapa, San Antonio Nuevo Paraíso, La Fortaleza y San Francisco La Paz. De manera muy especial quiero agradecer a todas las personas que me ayudaron en campo, Adrián, Prócoro, Diego, Paciano, Delfino, Raymundo, Rogelio, José, Valdemar y Lúcio, son los mejores guías en la selva de los Chimalapas (nunca me perdí), y siempre me consideraron como parte de su familia.

DEDICATORIA

A mis padres

María del Carmen y Vicente

Les amo mucho, son un ejemplo a seguir

A mis hermanos

Mirthe, Saúl y Bere

A ti Marisela

Moka te Amo, juntos hasta el final

ÍNDICE

PAG

CAPÍTULO II

Importance of large, old primary forest trees in nest-site selection by the Northern Mealy Amazon (*Amazona guatemalae*)....41

CAPITULO III

Differential value of forest types for foraging Northern Mealy Amazons in a fragmented landscape of tropical moist forest....61

CAPÍTULO IV.

RESUMEN

El estudio de los requerimientos ecológicos se engloba en el marco de la teoría de la distribución libre ideal y selección del hábitat. Para varias especies de psitácidos poco se conocen sus requerimientos ecológicos, y escasos estudios evalúan la selección de recursos. En este estudio se determinó el uso y selección de recursos como el hábitat, sitios de anidación y el alimento del loro corona azul (*Amazona guatemalae*), y cómo estos recursos influyen en la abundancia, estrategias de forrajeo y reproducción del loro, en la región de Los Chimalapas, Oaxaca. Asimismo, se evaluó si la especie sigue un modelo de distribución libre ideal según la disponibilidad de los recursos y las potenciales consecuencias para su éxito reproductivo.

Se determinó la abundancia y selección del hábitat por el loro al usar puntos de conteo en el bosque tropical perennifolio, bosque ribereño y bosque secundario. Asimismo, se evaluó si la estructura y composición de la vegetación influyen en la presencia y abundancia del loro. Para definir la dieta y selección de recursos alimenticios por el loro, se observó su forrajeo, y se establecieron 30 transectos de fenología para conocer la disponibilidad de recursos alimenticios en los tres tipos de vegetación. Por último, durante la época reproductiva, se ubicaron 40 nidos del loro. La selección de los sitios de anidación se determinó al comparar las características de los nidos con las cavidades accesibles registradas en 24 parcelas de 1 ha. Además, se hizo el seguimiento de los nidos para determinar la productividad reproductiva y la tasa de supervivencia diaria de los nidos. Finalmente, se comprobó si el loro sigue un modelo de distribución libre ideal al evaluar la relación de la disponibilidad de los recursos con la abundancia y el éxito reproductivo de los loros.

Nuestros resultados demuestran que el loro corona azul fue más abundante en la época reproductiva, mientras que durante la época no-reproductiva, el loro fue raramente observado

en la región. En la época reproductiva, la densidad del loro fue mayor en los bosques primarios con 35.9 loros/km^2 en el bosque ribereño y 18.9 loros/km^2 en el bosque perennifolio, comparado con tan solo 3.4 loros/km^2 en el bosque secundario. Además, el bosque secundario tuvo menor riqueza de especies de árboles, densidad, tamaño, altura total y altura de ramificación de los árboles comparada con los bosques primarios. El loro corona azul seleccionó el bosque ribereño, y su presencia y abundancia estuvo relacionada con la densidad de árboles de mayor diámetro y altura. Hubo variación espacio-temporal en la disponibilidad del alimento, el cual es menor durante la época no-reproductiva y en el bosque secundario. El loro mostró un nicho alimenticio amplio y consumió los recursos de acuerdo a su disponibilidad. La mayoría de los nidos del loro corona azul se registraron en árboles de *Terminalia amazonia* y *Dialium guianense*. Los loros seleccionaron para anidar cavidades a mayor altura, profundidad y diámetro interno, donde el diámetro interno y profundidad de la cavidad predicen el uso de una cavidad como nido. Sin embargo, solo 1.6 cavidades/ha tuvieron características adecuadas para la anidación del loro, y estas estuvieron concentradas en el bosque primario. Hubo una baja productividad y éxito reproductivo de los nidos principalmente por el saqueo de los pollos, donde los nidos localizados >3 km de los poblados humanos tuvieron mayor probabilidad de éxito.

Los resultados demuestran que el loro corona azul sigue un modelo de distribución libre ideal, la mayor densidad de los loros correspondió con la mayor disponibilidad de recursos (alimento y sitios de anidación) en hábitats conservados, y la ausencia del loro durante la época no-reproductiva coincidió con la declinación en fructificación de los árboles. Los resultados del estudio confirman que el loro corona azul depende de los bosques primarios, que brindan recursos alimenticios y sitios de anidación, influyendo en la distribución libre ideal del loro entre hábitats.

ABSTRACT

Research on ecological requirements falls within the framework of theories on ideal free distribution and habitat selection. For many species of parrots, little is known of their ecological requirements, and few studies have evaluated resource selection by parrots. In this study, we determined selection of habitats, nest-sites, and food resources by the Northern Mealy Amazon (*Amazona guatemalae*), and evaluated how resources influence the abundance, foraging strategies, and reproduction of this parrot species in Los Chimalapas, Oaxaca. In addition, we assessed whether the Northern Mealy Amazon follows an ideal free distribution model proportional to resource availability, and the potential consequences for the species' reproductive success.

The abundance and density of Northern Mealy Amazons was determined using point counts in evergreen, riparian, and secondary forests. Likewise, we assessed whether vegetation structure and composition influence presence and abundance of parrots at point counts, determined whether parrots selected forest types compared to their availability in the landscape. I observed foraging parrots to determine their diet, and selection of food resources. I also established 30 fruiting phenology transects to evaluate food resource availability for parrots in the three forest types. Additionally, I located 40 parrot nests during the breeding season. Dimensions of nest-cavities were compared with those of available cavities found in 24 1-ha survey plots to determine nest-site selection by parrots. Nest inspections were also conducted to determine reproductive output and daily nest survival rates. Finally, we evaluated the relationship of parrot abundance with resource availability to determine whether parrots follow an ideal free distribution model.

Our results demonstrate that the Northern Mealy Amazon was more abundant during the breeding season, whereas parrots were rarely observed in the region during the non-

breeding season. In the breeding season, density of Northern Mealy Amazon was higher in primary forests with 35.9 parrots/km^2 in riparian forest and 18.9 parrots/km^2 in evergreen forest, compared to only 3.4 parrots/km^2 in secondary forest. Secondary forest had lower tree species richness, density, tree size, total height and lower ramification height of trees compared to primary forests. Northern Mealy Amazons selected riparian forest, and their presence and abundance was related to density of large, tall trees. We found spatial-temporal variation in food resource availability, with fewer resources during the non-breeding season and in secondary forest. Parrots presented a broad dietary niche and consumed items according to their availability. The majority of Northern Mealy Amazon nests occurred in trees of *Terminalia amazonia* and *Dialium guianense*. Parrots selected nest-cavities at a greater height above the ground, with larger internal diameter, and greater depth, where internal diameter and cavity depth predicted use of a cavity as a nest-site by parrots. However, only 1.6 cavities/ha had characteristics suitable for use as nest-sites by parrots and these occurred in primary forest. Northern Mealy Amazons had low reproductive output and nest success, mainly due to nest poaching, where nests located >3km from human settlements had higher probability of success.

These results demonstrate that the Northern Mealy Amazon follows an ideal free distribution model, where higher parrot density corresponded with greater resource (food and nest-site) availability in primary forests, and the absence of parrots during the non-breeding season coincided with a decline in fruiting trees. Our results also confirm that the Northern Mealy Amazon depends on primary forests that provide food resources and nest-sites, influencing the abundance and distribution of parrots among habitats.

INTRODUCCIÓN GENERAL

Marco teórico sobre el estudio de los requerimientos ecológicos

Los requerimientos ecológicos, como el alimento, sitios de anidación y hábitat, son recursos necesarios en la supervivencia y reproducción de las especies (Andrewartha y Birch 1954, Tilman 1982, Wiens 1984, 1989, Newton 1998). En las aves, la mayoría de los estudios que han evaluado los requerimientos ecológicos se han enfocado sólo en el uso de los recursos, y pocos estudios han evaluado la selección de éstos (Johnson 1980, Jones 2001, Fuller 2012). Para determinar la selección, se necesita información del uso y de la disponibilidad de los recursos (Jones 2001, Manly et al. 2002). Así, la selección de recursos ocurre cuando una especie utiliza un recurso de modo desproporcionado a su disponibilidad (Johnson 1980, Jones 2001), y teóricamente las especies deben seleccionar los recursos de mejor calidad para cubrir sus requerimientos ecológicos (Jones 2001).

El estudio de los requerimientos ecológicos de las especies, se engloba en el marco de la teoría de la distribución libre ideal (Fretwell y Lucas 1969) y la selección del hábitat (Partridge 1978). La teoría de la distribución libre ideal supone que los individuos son “libres” de ocupar cualquier hábitat, y eligen de manera “ideal” el hábitat de mejor calidad para su adecuación. Así, dicha teoría predice que los individuos se distribuyen proporcionalmente entre hábitats según la disponibilidad de los recursos (Fretwell y Lucas 1969). Sin embargo, en el ambiente, los recursos no se encuentran distribuidos uniformemente, y muestran alta heterogeneidad entre parches (MacArthur y Pianka 1966). Bajo estas condiciones, los individuos deben utilizar con preferencia los parches óptimos que ofrecen mejores recursos y podrían mostrar selección del hábitat (MacArthur y Pianka 1966, Fretwell y Lucas 1969). Con relación a esto, la teoría de selección del hábitat refiere al uso desproporcionado de un hábitat sobre otro, donde hábitats de mejor calidad podrían incrementar la supervivencia y reproducción de los individuos (Hilden 1965, Partridge 1978, Cody 1985).

Las aves son buenos modelos para evaluar la selección del hábitat y los recursos, ya que tienen alta capacidad de movimiento entre distintos hábitats o parches de recursos. En las aves frugívoras, se ha observado que las variaciones espacio-temporales en la disponibilidad y abundancia de los recursos alimenticios influyen en su abundancia, movimientos y uso del hábitat (Levey 1988, Loiselle y Blake 1991, Whitney y Smith. 1998, de Paiva et al. 201). Respecto a los sitios de anidación, particularmente las aves que son anidadores secundarios de cavidades dependen de las cavidades existentes en los bosques para anidar, por lo cual la disponibilidad de este recurso puede limitar el número de parejas reproductivas y tamaño poblacional (Newton 1994, Cockle et al. 2010, 2011). En los requerimientos de hábitat, el alimento y los sitios de anidación son componentes claves en el uso y selección del hábitat por las aves (Whitney y Smith 1998, Badyaev et al. 1996, Jones 2001), y generalmente estos componentes se relacionan con la estructura de la vegetación (Rotenberry y Wiens 1980, Loyd 2004).

Un grupo de aves donde es interesante estudiar el efecto de las variaciones en la disponibilidad de los recursos son los psitácidos. Estas aves muestran amplia capacidad de movimiento y cubren distintos hábitats en sus movimientos diarios (Amuno et al. 2007, Stahala 2008, Ortiz-Maciel et al. 2010), por lo cual podrían mostrar selección del hábitat según la disponibilidad de los recursos (Salinas-Melgoza y Wright 2013). Los estudios que han evaluado los requerimientos de hábitat en los psitácidos, indican que particularmente las especies de mayor tamaño muestran mayor asociación y abundancia en bosques primarios, con mayor biomasa arbórea y mejor estado de conservación (Marsden y Fielding 1999, Kinnaird et al. 2003, Evans et al. 2005, Marsden y Symes 2006, Legault et al. 2011).

Asimismo, la mayoría de los psitácidos son principalmente granívoros del dosel y pueden consumir una variedad de especies de plantas (Galetti 1993, Simão et al. 1997, Renton 2001, Matuzak et al. 2008) que muestran variación espacial y temporal en su productividad (Hilty 1980, Loiselle y Blake 1991). Por lo tanto, los psitácidos deben ajustar la búsqueda de los recursos alimenticios al seguir su disponibilidad en el ambiente (Renton 2001), y poder seleccionar aquellas especies de plantas que brinden mejores beneficios energéticos (Crowley y Garnett 2001, Renton 2006, Brightsmith et al. 2010, Díaz et al. 2012). Además, se ha sugerido que los psitácidos pueden realizar movimientos entre hábitats como estrategia frente a cambios en la disponibilidad de los recursos alimenticios (Greene 1998, Renton 2001, Morales-Pérez 2005).

Por otro lado, el 76% de las especies de psitácidos son anidadores secundarios de cavidades (Forshaw 1989, Renton et al. 2015), por lo que dependen de la disponibilidad de cavidades con condiciones adecuadas para su anidación y éxito reproductivo (Cockle et al. 2008, 2011). Sin embargo, pocos estudios han determinado la disponibilidad de los sitios de anidación para los psitácidos. Los estudios que han comparado las características de cavidades utilizadas como nidos con las cavidades disponibles, coinciden en que los psitácidos seleccionan los sitios de anidación con base en la altura, tamaño y profundidad de las cavidades (Snyder et al. 1987; Enkerlin-Hoeflich 1995; Stojanovic et al. 2012, de la Parra-Martínez et al. 2015). Aunque para la mayoría de las especies se desconoce si realizan selección de sitios de anidación con base en las características de las cavidades.

Por último, los psitácidos representan el grupo de aves con la mayor proporción de especies amenazadas y en riesgo de extinción (Bennett y Owens 1997, BirdLife

International 2016a). Tan solo en el Neotrópico, 176 especies (37% del total) se encuentran en alguna categoría de riesgo (Olah et al. 2016), en particular la situación de las especies del género *Amazona* es crítica (Snyder et al. 2000). En México, 10 especies y 3 subespecies de psitácidos se encuentran en peligro de extinción, 6 como amenazadas y 4 sujetas a protección especial (SEMARNAT 2010). Las principales causas que han originado el estatus de riesgo en los psitácidos son los impactos antropogénicos sobre el hábitat de las especies, y la captura ilegal para el comercio de mascotas (Snyder et al. 2000, Olah et al. 2016).

Por este motivo, evaluar los requerimientos ecológicos del hábitat, recursos alimenticios y sitios de anidación, pondría en evidencia las características que hacen a ciertas especies vulnerables a la perturbación del hábitat por actividades antropogénicas, y por el contrario se podría identificar por qué otras especies son flexibles a la perturbación del hábitat y persisten en bosques modificados (Saunders 1990, Sodhi et al. 2008). Respecto a esto último, es importante determinar si una mayor plasticidad en el uso de recursos permite a las especies adaptarse o presentar mayor tolerancia a la perturbación (Saunders 1990, Julliard et al. 2006).

El loro corona azul

Recientemente, el loro corona azul (*Amazona guatemalae*) fue separado taxonómicamente de la especie *A. farinosa* (BirdLife International 2016a). Además, análisis genéticos demuestran dos grupos distintos de especies crípticas en América Sur y Central (Wenner et al. 2012, del Hoyo y Collar 2014). La distribución de *A. guatemalae* ocurre desde el sureste de México hasta el oeste de Panamá en Centroamérica (BirdLife International 2016b). Cabe destacar que la reciente designación de *A. guatemalae* como especie independiente impulsa la necesidad de re-evaluar su estado de conservación.

Actualmente, el loro corona azul es considerado como una especie casi amenazada en la lista roja de la UICN (BirdLife International 2016b), y en México es clasificado en peligro de extinción (SEMARNAT 2010). No obstante, tan solo en México la especie ha sufrido una reducción del 46.8% en su distribución original (Monterrubio-Rico et al. 2016), principalmente por la pérdida de hábitat (Collar y Juniper 1992, De Labra et al. 2010). Además, la especie está amenazada por la alta presión del saqueo de nidos (Cantú et al. 2007, Lira-Torres et al. 2014). Por tanto, podría ocurrir que las poblaciones del loro corona azul en Mesoamérica enfrenten mayor presión por la pérdida del hábitat y el tráfico ilegal de mascotas, que las poblaciones del sur del continente (*A. farinosa*).

El loro corona azul habita principalmente en tierras bajas (0–1000 msnm) particularmente en el bosque primario (Binford 1989, Forshaw 1989, Howell y Webb 1995, Domínguez y Ruelas-Inzunza 1996), aunque aún no se han evaluado los requerimientos de hábitat de la especie. A pesar de ser la especie de loro *Amazona* más grande de Mesoamérica (Forshaw 1989), el conocimiento de sus requerimientos ecológicos es casi nulo. La información publicada sobre la dieta del loro es limitada, donde sólo se cuenta con un reporte de alimentación de semillas de *Brosimum utile* en Costa Rica (Higgins 1979), y un listado de 33 especies de plantas en Petén, Guatemala (Bjork 2004). Sin embargo, estos estudios no indican si la disponibilidad de los recursos alimenticios influye en la abundancia del loro y en el uso del hábitat. Respecto a los requerimientos de anidación, se reporta que la especie anida en huecos de 22 especies de árboles (Bjork 2004). Sin embargo, se desconocen los requerimientos de anidación y si la especie selecciona los sitios de anidación con base en sus características. Además, se sabe que este psitácido realiza movimientos estacionales de larga distancia (138 ± 61.9 km), desde Petén en Guatemala hasta bosques húmedos del sur de México, patrón que coincide con la declinación de recursos alimenticios en Tikal (Bjork 2004).

Debido a que poco se conocen los requerimientos ecológicos del loro corona azul, su estudio ayudaría a determinar la vulnerabilidad a los factores de riesgo y las posibles amenazas para la persistencia a largo plazo de esta especie amenazada. Esta información novedosa será clave para desarrollar estrategias precisas de conservación del loro.

Los Chimalapas

Los Chimalapas se ubica al noreste del estado de Oaxaca (17°08' - 17°04' N y 94°36' - 94°08' O). Políticamente limita al norte con la región del Uxpanapa en Veracruz, y al este con la región El Ocote, en Chiapas. Los Chimalapas es una de las regiones tropicales de mayor importancia biológica en México y Mesoamérica (Wendt 1987, Arizmendi y Márquez 2000, Arriaga et al. 2000, Peterson et al. 2003, Navarro Sigüenza et al. 2008). En Los Chimalapas, anualmente ocurren variaciones en la precipitación entre 2,000-4,500 mm, con fluctuaciones en la temperatura entre 22-26°C, y se presenta una estación seca muy corta de marzo a junio (Trejo 2004). La vegetación que predomina es el bosque tropical perennifolio, que ocupa aproximadamente el 45.7% de la superficie (2,604.2 km^2), con las especies arbóreas comunes: *Ficus insipida*, *Brosimum alicastrum*, *Dialium guianense*, *Terminalia amazonia*, *Cojoba arborea*, *Calophyllum brasiliense* y *Guarea glabra* (Torres Colín 2004). Otro tipo de vegetación es el bosque ribereño conformado por agrupaciones arbóreas heterogéneas que se desarrollan a lo largo de corrientes de agua (Rzedowski 1978, De la Maza 1989). Sin embargo, en años recientes extensas áreas del bosque primario fueron removidas producto de actividades antropogénicas y actualmente son áreas con vegetación en diferentes etapas de sucesión secundaria, conocida localmente como "acahual" (Rzedowski 1978, Torres Colín 2004).

Sitios de estudio

Con base en registros históricos de la presencia del loro corona azul (*Amazona guatemalae*) en la región (Binford 1989, Howell y Webb 1995) y un monitoreo previo realizado en noviembre del 2012, se identificaron y seleccionaron cuatro sitios. Estos sitios presentan distintas condiciones de estado de conservación de la vegetación como resultado de diferentes prácticas antropogénicas.

Chalchijapa. Se ubica al noroeste de la región (17° 3' 25.5''N - 94° 39' 34.7''O) a 260 msnm. El sitio está cubierto por bosque tropical perennifolio en sistemas montañosos conectadas por el bosque ribereño lo largo de ríos. El bosque primario está rodeado por extensas áreas de potreros con pastizales introducidos y vegetación secundaria. La principal actividad es la ganadería extensiva y la tala selectiva. La comunidad está constituida por 203 habitantes (INEGI 2015).

San Antonio. Se ubica al norte de la región (17° 9' 32.2''N - 94° 13' 45.3''O) a 289 msnm. El sitio cuenta con extensas áreas cubiertas por el bosque tropical perennifolio conservado y en menor proporción por vegetación secundaria (acahuales y potreros con pastizales), siendo uno de los sitios más conservados de la región. En este sitio la degradación de los bosques ha ocurrido durante los últimos 15 años. La principal actividad es la ganadería extensiva. El sitio fue poblado hace aproximadamente 25 años, y la comunidad está constituida por 106 habitantes (INEGI 2015).

San Francisco. Se ubica al noreste de la región de Los Chimalapas (17° 5' 44.5''N - 94° 7' 8.4''O) a una altitud de 77 msnm. El sitio está conformado principalmente por vegetación de entre 15 a 25 años de sucesión secundaria, áreas no degradadas del bosque tropical perennifolio en sistemas montañosos, así como fragmentos del bosque primario en montañas de baja altitud. Este sitio muestra la mayor degradación de los bosques, con extensas áreas ocupadas por potreros con pastizales para uso ganadero. Además por su baja altitud, gran parte del terreno es utilizado para el cultivo de maíz. La comunidad está constituida por 628 habitantes (INEGI 2015).

La Fortaleza. Se ubica al noreste de la región (17° 9' 32.2''N - 94° 13' 45.3''O) a una altitud de 80 msnm. Este sitio está rodeado por montañas pedregosas y cañadas en las que predomina el bosque tropical perennifolio rodeado por vegetación secundaria y pastizales introducidos. La principal actividad es la ganadería extensiva y en menor medida cultivos de maíz, frijol y calabaza. Este sitio fue fundado hace aproximadamente 33 años y la comunidad está formada por alrededor de 194 habitantes (INEGI 2015).

Estado de conservación de la vegetación en Los Chimalapas

Los Chimalapas, junto con la selva Lacandona, forman los dos grandes relictos del bosque tropical perennifolio en México, que cubre actualmente el 10% del área histórica de dicho bosque (Masera et al. 1997, Challenger 1998). La destrucción del bosque primario en Los

Chimalapas, aunque explotado desde la colonización española, es un fenómeno relativamente reciente. Hasta finales de los noventas, el 78.3% (4,651 km^2) de la superficie de Los Chimalapas correspondía a vegetación conservada de bosques primarios, principalmente de bosque perennifolio (Salas-Morales et al. 2001). Recientemente, un estudio sobre el monitoreo del cambio del uso del suelo durante el 2000-2003, indica que el bosque perennifolio cubre el 45.7 % (2,604.2 km^2) de la superficie de Los Chimalapas. Durante este periodo, se perdió aproximadamente el 32.6% (2046.8 km^2) del área total que cubría este bosque, y actualmente se estima que la tasa anual de pérdida de los bosques primarios es del 5.8% (Martínez-Pacheco 2012).

En gran medida, en la región de Los Chimalapas la degradación de los bosques es producto de la ganadería extensiva que se practica dentro de una superficie de 164.7 km^2, por la tala selectiva de árboles maduros y por los incendios forestales. A menor escala, la degradación de los bosques también es producto de la siembra de maíz, plantación de árboles de hule y la apertura de caminos para carreteras. A nivel espacial, la tala selectiva para la venta de madera es la principal actividad y fuente de ingresos económicos en las localidades ubicadas en el centro de la región, mientras la ganadería es la principal actividad en las localidades del este y oeste de la región (Arriaga et al. 2000, Martínez-Pacheco 2012). En conclusión, en la región de Los Chimalapas, la expansión de la ganadería, la tala selectiva, los desmontes para siembra de pastos y la apertura de caminos para carreteras, es una amenaza constante para mantener la continuidad entre los bosques y conservar la biodiversidad.

Por lo tanto, evaluar los requerimientos ecológicos del loro corona azul bajo distintas condiciones de conservación de la vegetación en la región de los Chimalapas, permitiría reconocer las características del hábitat que influyen en la abundancia, dieta y reproducción del loro. Además, debido a que en México es constante la conversión de los bosques tropicales por áreas agrícolas (de Jong et al. 2010), en el futuro esta información será clave en la toma de decisiones para la regularización del manejo de los bosques en el área de estudio y en general del área de distribución del loro corona azul en Mesoamérica.

Metas y objetivos del estudio

La meta general del presente estudio es determinar los requerimientos ecológicos del loro corona azul (*Amazona guatemalae*) en la región de los Chimalapas, con el propósito de entender los procesos de selección de recursos específicos como el hábitat, recursos alimenticios y sitios de anidación. Asimismo, se pone a prueba si el loro corona azul sigue un modelo de distribución libre ideal en el uso de los recursos. Por ello, el presente estudio es el primer esfuerzo por determinar el uso y selección de recursos por el loro, para ello, el estudio se estructuró en cuatro capítulos.

En el capítulo I se determinará la densidad y selección del hábitat, y se analizarán las características de la vegetación que influyen en la presencia y abundancia del loro. En el capítulo II se determinará si el loro corona azul selecciona sitios de anidación al comparar las características de los nidos con las cavidades disponibles registradas en tres tipos de vegetación. En el capítulo III se presentaran las estrategias de forrajeo empleadas por la especie al evaluar la dieta y la disponibilidad de los recursos alimenticos a nivel espacial y temporal. Finalmente, en el capítulo IV se incluirá información de la productividad y se reportarán los factores que influyen en el éxito reproductivo de la especie, asimismo se relacionará la disponibilidad de los recursos (alimento y cavidades) con la abundancia y el éxito reproductivo del loro para poner a prueba la distribución libre ideal de la especie.

CAPÍTULO I

(Sometido para publicación en *Avian Conservation and Ecology*)

Factors influencing density of the Northern Mealy Amazon in three forest types of a modified rainforest landscape in Mesoamerica

Miguel Ángel De Labra-Hernández[1] and Katherine Renton[2]

[1]Posgrado en Ciencias Biológicas, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico.

[2]Estación de Biología Chamela, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 21, San Patricio-Melaque, Jalisco, Mexico.

Corresponding Author: K. Renton (krenton@ib.unam.mx)
Telephone & Fax: 52-315-3510202

Estado del proceso: *Finalización de revisiones solicitadas por los árbitros y reenviado al Editor*

ABSTRACT

The high rate of conversion of tropical moist forest to secondary forest makes it imperative to evaluate forest metric relationships of species dependent on primary, old-growth forest. The threatened Northern Mealy Amazon (*Amazona guatemalae*) is the largest mainland parrot, and occurs in tropical moist forests of Mesoamerica that are increasingly being converted to secondary forest. However, the consequences of forest conversion for this recently taxonomically separated parrot species are poorly understood. We measured forest metrics of primary evergreen, riparian, and secondary tropical moist forest in Los Chimalapas, Mexico. We also used point counts to estimate density of Northern Mealy Amazons in each forest type during the non-breeding (Sept 2013) and breeding (March 2014) seasons. We then examined how parrot density was influenced by forest structure and composition, and whether parrots selected forest types within tropical moist forest. Overall, parrot density was high in the breeding season, with few parrots present during the non-breeding season. During the breeding season, primary forest had significantly greater density of 18.9 parrots/km^2 in evergreen forest and 35.9 parrots/km^2 in riparian forest, compared to only 3.4 parrots/km^2 in secondary forest. Secondary forest had significantly lower tree species richness, density, diameter, total height, and major branch ramification height, as well as distinct tree species composition compared to both types of primary forest. The number of Northern Mealy Amazons recorded at point counts was related to density of large, tall trees, characteristic of primary forest, and parrots selected riparian forest along permanent rivers. Hence, the increased conversion of tropical moist forest to secondary forest is likely to lead to reduced densities of forest-dependent species such as the Northern Mealy Amazon. Furthermore, the species' requirement for primary tropical moist forest highlights the need to reevaluate conservation status of the Northern Mealy Amazon, and implement strategies to reduce forest conversion.

Key words: *Amazona guatemalae*; *conservation ecology*; *General Additive Models, habitat selection*; *forest structure and composition; Psittacidae*; *secondary forest conversion*; *tropical moist forest*;

INTRODUCTION

Land transformation due to anthropogenic activities affects almost half the earth's surface, and is the primary driving force in the loss of biodiversity (Vitousek et al. 1997). Tropical moist broadleaf forest has one of the highest rates of deforestation and conversion, and is increasingly being reduced to forest remnants within a mosaic of agricultural land (Skole and Tucker 1993, de Jong et al. 2010). Species richness of birds declines with increasing forest disturbance (Lawton et al. 1998), and bird species that mainly inhabit forests are particularly prone to extinction risk (Şekercioğlu et al. 2004). This makes it imperative to evaluate avian habitat relationships of tropical species dependent on primary, old-growth forest that may be vulnerable to increased forest loss and conversion to secondary forest (Brook et al. 2006, Wright and Muller-Landau 2006*a*,*b*).

Almost a third of Psittaciformes (parrots) are currently threatened (BirdLife International 2016*a*), the majority of which occur in the Neotropics (Olah et al. 2016). Among these, the genus *Amazona* has the greatest species richness, two thirds of which are internationally considered threatened (Snyder et al. 2000). The main cause of decline for the majority of threatened Psittaciformes is through anthropogenic impacts of agriculture, capture for trade, and logging, with large-bodied, forest-dependent parrot species more likely to be threatened (Olah et al. 2016). Large-bodied parrot species exhibit low population densities, and tend to be associated with primary forests (Marsden 1999, Marsden and Pilgrim 2003, Symes and Marsden 2007, Lee and Marsden 2012). In particular, forest structural characteristics of tree diameter, height, and canopy cover influence psittacine density (Marsden 1992, Evans et al. 2005, Marsden and Symes 2006). Nevertheless, the majority of studies have been conducted on Psittaciformes of Papua New Guinea and the Indonesian islands (Marsden and Royle 2015), and we have very limited information on the response to forest conversion of threatened parrot species in tropical moist forests of continental America.

The Near Threatened Northern Mealy Amazon (*Amazona guatemalae*) is one of the largest Amazon parrot species in continental America, and occurs in Central America from southern Mexico to western Panama (Forshaw 1989, Birdlife International 2016*b*). Given that the Northern Mealy Amazon has only recently been taxonomically separated from the more widely distributed Southern Mealy Amazon (*Amazona farinosa*) in South America (Wenner et al. 2012, del Hoyo and Collar 2014), it is essential to determine the status and ecological requirements of the Northern Mealy Amazon in Central America. However, only one study has been conducted on the Northern Mealy Amazon, which determined that the species undertakes long-distance seasonal movements from the Petén in Guatemala to tropical moist forest in southern Mexico (Bjork 2004).

Forest conversion is one of the main factors affecting wild populations of the Northern Mealy Amazon, and in Mexico the species has been extirpated from a large part of its historic range, suffering a 45% reduction from its original distribution (Ríos-Muñoz and Navarro-Sigüenza 2009, De Labra et al. 2010). The tropical moist forest of the Chimalapas region in northeastern Oaxaca, Mexico, is one of the most biologically diverse areas in Mesoamerica, and has been largely unstudied (Peterson et al. 2003, Navarro-Sigüenza et al. 2008). However, tropical moist forest in this region is increasingly threatened by anthropogenic activities of selective forestry, and land conversion for agriculture or cattle grazing (Martínez-Pacheco 2012).

In the present study, we aimed to evaluate forest metrics associated with density of Northern Mealy Amazons, and determine whether parrots selected forest types in the modified landscape of Los Chimalapas, Mexico. We hypothesized that the large-bodied Northern Mealy Amazon would occur at low density, and be associated with primary tropical moist forest, that is characterized by a high density of large, tall trees. Therefore, specific objectives of our study were to: 1) determine density of Northern Mealy Amazons in three forest types of primary evergreen tropical moist forest (evergreen hereafter), primary riparian tropical moist forest (riparian hereafter), and tropical moist forest at various stages of secondary succession (secondary hereafter); 2) identify differences among forest types in metrics of forest structure and tree species richness; 3) evaluate relationships of metrics of forest structure and tree species composition with occurrence and number of parrots at point counts; and 4) determine whether use of forest types by Northern Mealy Amazons differed from availability of forest types in the landscape. In this way, we aimed to identify forest types with high parrot density that are selected by Northern Mealy Amazons, and forest metrics that influence parrot density, so as to guide management and conservation for this large, threatened parrot species.

METHODS

Study area

We conducted the study in the highland region of Los Chimalapas (17°08' - 17°02' N, 94°38' - 94°08' W; Fig. 1) in northeastern Oaxaca, Mexico. The 6,000 km^2 region of Los Chimalapas is owned and managed by the Zoque indigenous group. The Northern Mealy Amazon occurs in northern Chimalapas, in the Municipality of Santa Maria Chimalapa, which is located within the tropical moist broadleaf forest biome (Olson et al. 2001). Annual rainfall is 2,000-4,500 mm, with average temperatures 22-26°C, and a short dry season from March to June (Trejo 2004). The region has an elevation range of 70-1800 m asl, where primary tropical moist forest covers 45.7% of the landscape (Torres Colín 2004).

Within primary tropical moist forest, we surveyed two forest types of evergreen and riparian, of which primary evergreen forest comprised the largest area of 1728.7 km^2 in Santa Maria Chimalapa. Common tree species of evergreen forest are *Dialium guianense*, *Terminalia amazonia*, and *Cojoba arborea* (Torres Colín 2004). Riparian forest occurred along permanent rivers, mainly below 500 m asl, and comprised 491.9 km^2 of land cover in Santa Maria Chimalapa. Common tree species of riparian forest are *Ficus* sp., *Garcinia macrophylla*, *Vochysia guatemalensis*, and *Inga vera* (Torres Colín 2004). Anthropogenic activities in Santa Maria Chimalapa have promoted a high rate of conversion of primary tropical moist forest, with transformation of 7.3 km^2 of primary forest per year during 2000-2003 (Martínez-Pacheco 2012). This has resulted in tropical moist forest at various stages of secondary succession, with secondary forest comprising 420.6 km^2 of land cover in Santa Maria Chimalapa by 2003 (Martínez-Pacheco 2012). We surveyed parrots and measured forest metrics at point counts in evergreen, riparian, and secondary forest below 600 m asl, across a 60 km section of northern Chimalapas in the Municipality of Santa Maria Chimalapa.

Parrot surveys

To determine the density of Northern Mealy Amazons in the modified landscape of Los Chimalapas, we established 120 variable radius point counts, stratified as 60 in primary forest, and 60 in secondary forest. Within the primary forest, we located 33 point counts in tropical evergreen forest and 27 point counts in riparian forest along permanent rivers. Point counts were separated by 250 m to increase independence of counts (Marsden 1999). Reproductive activity of the Northern Mealy Amazon commences in January with nest-site selection and copulation by breeding pairs (Bjork 2004). Nests are initiated in late-February with the start of egg-laying, and nesting continues through to early July when the last chicks fledge (Bjork 2004). Therefore, we conducted surveys of parrots in the non-breeding season of September 2013, and in the breeding season of March 2014.

All surveys were conducted by MADLH, and each point count was surveyed only once in both the breeding and non-breeding season. We conducted a 10 min count at each point to increase the likelihood that birds close to the observer were detected (Marsden 1999). We recorded all parrots seen or heard, and noted the number of parrots, form of detection (observation, vocal), whether the parrot was perched, and compass direction of the detection. We also measured distance from the observer to the bird with a Bushnell Yardage Pro 450 range-finder. Surveys were conducted after sunrise and until 10:30 h, which is the period of greatest parrot activity (Marsden 1999).

Forest structure and composition

At each point count we marked out a 25 m-radius circular plot to survey forest structure, and composition in an area of 1,963.5 m^2 around the point. Within this survey plot we determined the number of trees with diameter at breast height (dbh) ≥10 cm. We considered 10 cm dbh as the lower limit for trees recorded in our surveys as this is frequently used in forest surveys (Bullock and Solis-Magallanes 1990, Chapman et al. 1994), and large trees are more likely to be used by the Northern Mealy Amazon, which is a large-bodied canopy species (Greenberg 1981, Loiselle 1988, Bjork 2004). For each tree, we measured dbh at 1.3 m height using a 10 m diameter tape, and determined total tree height, and ramification height to the first major branch, using a tree-measuring pole extendable to 15 m for trees <15 m height, and a Criterion RD 1000 digital dendrometer for trees >15 m height. Trees that ramify at over half their total height are indicative of having grown in shady closed-canopy conditions of primary forest, whereas trees that ramify at less than half their total height are indicative of having grown in more open conditions of disturbed or secondary forests (Torquebiau 1986). These variables of forest structure could therefore provide an indication of the condition of forests around each point count.

We also identified tree species within each 25 m-radius circular plot using reference guides of Pennington and Sarukhán (1998), and Vázquez Torres et al. (2010). Where tree species could not be identified in the field, we collected samples for identification in the Herbario Nacional of the Instituto de Biología, Universidad Nacional Autónoma de México in Mexico City. In particular, we recorded the abundance of tree species used as resources by mealy parrots (*A. guatemalae*, and *A. farinosa*), as abundance of tree species used as food or nest-site resources has been found to influence occurrence and density of other parrot species (Kinnaird et al. 2003, Berkunsky et al. 2015). Tree species occurring in Santa Maria Chimalapa that have been reported in the diet or used as nest-sites by mealy parrots (Bjork 2004, Lee et al. 2014) include *Terminalia amazonia*, *Dialium guianense*, *Ficus* sp., *Spondias mombin*, *Ochroma pyramidale*, and *Sloanea meianthera* (Table A1.1).

Statistical analyses

We used records of parrots that were perched (Marsden 1999) to estimate parrot density per forest type using the program Distance 6.0 (Thomas et al. 2006). We used the Multiple Covariates Distance Sampling engine of Distance 6.0 both to increase the reliability of density estimates where there may be few observations in a subset of data by forest type, and to enable inferences regarding covariates of forest structure (Marques et al. 2007). We included the forest structure covariates of tree density, mean tree dbh, and mean tree height recorded at each point count. However, we excluded mean tree ramification height to the first major branch as this was strongly correlated with total tree height ($r = 0.81$, $P < 0.5$), and highly correlated variables may lead to bias in density estimates (Marques et al. 2007). Data were not truncated so as to include the greatest number of detections of perched birds. We used a stratification approach to analyze survey data by forest type, and generated distance models using the half-normal and hazard functions, with cosine and simple polynomial series adjustments, and all combinations of covariates. We then selected the most appropriate density model based on the lowest Akaike Information Criteria (AIC; Buckland et al. 2001), and calculated delta Akaike (ΔAIC) to identify additional candidate models (Table A1.2).

Using the distance model with lowest AIC that had best fit to the data, we obtained Northern Mealy Amazon density estimates, and their 84% confidence intervals, for each forest type. Density estimates were considered to differ significantly among forest types where upper and lower 84% confidence intervals did not overlap, as this robustly mimics the 0.05 probability obtained from statistical tests (Payton et al. 2003, MacGregor-Fors and Payton 2013).

To determine whether forest types differed in species richness and forest structure around point counts, we compared metrics of tree species richness, tree density, mean tree dbh, mean tree height, and mean ramification height among evergreen, riparian, and secondary forests. Data did not present a normal distribution, therefore we applied Kruskal-Wallis ANOVA to compare metrics among forest types. Where significant differences were detected, we applied Dunn post-hoc analysis to determine which forest type contributed the significant difference (Zar 1999). We also calculated the Morisita index of similarity to compare the abundance of each tree species among the three forest types (Krebs 1999).

To evaluate relationships of the complete set of forest structure and tree species composition metrics with occurrence and number of parrots recorded at point counts, we first used principal component analysis (PCA) to convert 11 forest metrics to a reduced set of composite axes. These included 4 forest structure variables of tree density, mean dbh, mean tree height, and mean ramification height, as well as 7 floristic composition variables of tree species richness, and the abundance of each of the 6 common tree species used as resources by mealy parrots (*T. amazonia*, *D. guianense*, *Ficus* sp., *S. mombin*, *O. pyramidale*, and *S. meianthera*). We retained only the principal components with eigenvalues >1, which were incorporated as predictor variables in generalized additive models (GAMs) to evaluate their relationships with number of parrots and presence/absence of parrots at point counts. We used GAMs as these are less restrictive, generating non-linear response curves that are modelled as a series of additive smoothing functions dictated by the data (Hastie and Tibshirani 1986). This is more suited to deal with non-linear complex relationships that may occur in nature. We fitted penalized cubic regression splines to the data to control complexity of the curve (degrees of freedom) and avoid overfitting (Wood 2006). We used the 'mgcv' package in R (Wood 2011; R Core Team 2016) to run Poisson GAMs to model the relationship with number of parrots recorded at point counts, and binomial GAMs to model the presence/absence of parrots perched within a 50 m radius of the point count. The model which presented the lowest AIC was selected as the model that best explained deviance in the data, and we calculated ΔAIC, and Akaike weights (*wi*) to identify competing models (Burnham and Anderson 2002).

Finally, to determine whether use of forest types by Northern Mealy Amazons differed from that expected by availability, we applied *G*-test to compare the number of parrots recorded in each forest type with the number of parrots expected based on availability of forest types. For observed use in each forest type, we considered only parrots perched within a 50 m radius around each point count. We determined proportional availability of each forest type using estimates of land-cover area determined for Santa Maria Chimalapa municipality in Los Chimalapas by Martínez-Pacheco (2012) based on 28.5 m resolution Landsat ETM satellite images from 2000-2003. For secondary forest, we combined the area estimates for the two categories of degraded and secondary forest classified by Martínez-Pacheco (2012). We calculated riparian forest cover considering a 50 m band-width at each side of permanent rivers in the study area, which were overlaid from a hydrogeological map of 1:250,000 (INEGI 2012) using the QGIS 2.12 Geographic Information System (QGIS Development Team 2015). To obtain the expected number of parrots in each forest type, we multiplied the total number of parrots recorded over all forest types by the proportional land cover of each forest type. This gave the number of parrots that would be expected in each forest type based on the proportional availability of that forest type in the landscape, which was compared with the observed number of parrots recorded in each forest type.

To determine whether a particular forest type was selected by parrots we generated simultaneous Bonferroni confidence intervals for the proportional use observed for each forest type, using an alpha adjusted to $P < 0.017$ for the set of three forest types (Nue et al. 1974, Byers et al. 1984). Utilization differs significantly when the expected proportion of use based on availability falls outside the adjusted alpha confidence interval of actual use (Byers et al. 1984), with the resource category being used either more or less than expected by availability. All statistical analyzes were carried out using R version 3.3.0 (R Core Team 2016). Descriptive statistics are presented as mean with standard deviation, except where stated, and we considered $P < 0.05$ as significantly different in statistical analysis.

RESULTS

Parrot density

We obtained 133 detections of Northern Mealy Amazons in Los Chimalapas, although the majority of these were obtained during the breeding season with a total of 128 detections in March 2014, compared to only 5 detections during the non-breeding season of September 2013. During the breeding season, detections were made at a mean distance of 47.7 ± 28.9 m (range = 17-120 m, n = 29) in evergreen forest, 37.8 ± 22.2 m (range = 4-90 m, n = 46) in riparian forest, and 85.8 ± 57.9 m (range = 5-254 m, n = 53) in secondary forest. We recorded a mean 3.1 ± 3.6 parrots per 10 min point count in the breeding season, with a mean group size of 2.8 ± 2.3 parrots (range = 1-12 parrots). By comparison, parrots were largely absent from the study site during the non-breeding season, recording an average of only 0.15 ± 1.0 parrots per 10 min point count in September 2013, with a mean group size of 4.6 ± 2.9 parrots (range = 2-9 parrots). Therefore, it was not possible to model Northern Mealy Amazon density in the non-breeding season, and density estimates were conducted only for the breeding season.

The Distance model with the lowest AIC included two covariates of tree density and mean tree height, using the half-normal probability function with cosine adjustment (Table A1.2). This model estimated an overall mean density of 19.5 ± 6.2 Northern Mealy Amazons/km^2 during the breeding season (Table 1). Density estimates of parrots were significantly higher in both types of primary forest, with 18.9 ± 5.7 parrots/km^2 in evergreen forest, and 35.9 ± 8.7 parrots/km^2 in riparian forest, compared to only 3.4 ± 0.8 parrots/km^2 in secondary forest (Fig. 2).

Forest structure and composition

Forest structure within a 25-m radius of point counts differed significantly among forest types (Fig. 3). Secondary forest had significantly fewer trees ($H_2 = 62.7$, $P < 0.001$; Fig. 3A) than evergreen ($q = 5.0$, $P < 0.001$) and riparian ($q = 7.4$, $P < 0.001$) forests. Tree density in riparian forest was also significantly greater than evergreen forest ($q = 2.5$, $P < 0.05$; Fig 3A). Moreover, forest types differed in mean tree dbh ($H_2 = 18.8$, $P < 0.001$; Fig. 3B), total height ($H_2 = 40.8$, $P < 0.001$; Fig. 3C), and ramification height ($H_2 = 54.3$, $P < 0.001$; Fig 3D). In all cases, secondary forest differed from the two primary forest types (Fig 3), having trees of smaller dbh (Evergreen: $q = 4.3$, $P < 0.001$, Riparian: $q = 2.0$, $P < 0.05$), with lower total height (Evergreen: $q = 6.4$, $P < 0.001$, Riparian: $q = 2.8$, $P < 0.01$), and lower ramification height (Evergreen: $q = 6.9$, $P < 0.001$, Riparian: $q = 4.8$, $P < 0.001$). Furthermore, within primary forest, trees in evergreen forest had significantly greater total height ($q = 2.9$, $P < 0.01$) than trees in riparian forest (Fig 3C).

Species richness of trees was also significantly lower in secondary forest ($H_2 = 42.6$, $P < 0.001$) compared to evergreen ($q = 5.6$, $P < 0.001$) and riparian ($q = 4.9$, $P < 0.001$) forests (Fig. 3E). Tree species composition was similar between evergreen and riparian forest (Morisita = 0.66), whereas secondary forest differed in species composition compared to evergreen (Morisita = 0.42) and riparian forest (Morisita = 0.46). The most abundant tree species in evergreen forest were *Terminalia amazonia* and *Dialium guianense* (Fig. 4A), and these were also among the most abundant tree species in riparian forest (Fig. 4B). By comparison, the most common tree species in secondary forest was the fast-growing *Schizolobium parahyba* (Fig. 4C).

Relationship of forest metrics with parrot occurrence

The 11 forest structure and composition variables were reduced to three principal components that explained 94.8% of the variation (Table 2). The variable with greatest loading on principal component 1 was mean tree dbh, whereas component 2 was influenced by tree density, and component 3 was explained by mean tree height (Table 2). Model selection revealed a single candidate model for number of parrots at point counts, which incorporated all three principal components, and explained 73.8% of the deviance (Table A1.3a). Therefore Northern Mealy Amazon density during the breeding season is most likely influenced by forest structure of a high density of large, tall trees.

Inclusion of all three principal components in a single model also had the best fit for data on occurrence of parrots within a point count radius of 50 m, and explained 34.9% of deviance (Table A1.3b), with a 52.7% likelihood of being the best model. A competing model for parrot presence was comprised of principal components 1 and 2 (Table A1.3b), and had an almost equal 45.4% likelihood of being the best model. Therefore, parrots may be more likely to perch within 50 m of a point count in forest with a high density of large trees.

Finally, use of forest types by Northern Mealy Amazons differed significantly from that expected by availability of forest types in the landscape ($G_2 = 40.5$, $P < 0.001$). Northern Mealy Amazons were most frequently recorded in evergreen and riparian forest, but selected riparian forest using this more than expected by availability. By comparison, very few parrots were recorded within 50 m of point counts in secondary forest, and this forest type was used less than expected by availability (Table 3).

DISCUSSION

Parrot density

During the breeding season we recorded an overall density of 19.5 ± 6.2 Northern Mealy Amazons/km^2 in the tropical moist forest of Los Chimalapas, Mexico, with greatest density in primary forest. This is relatively high compared to other large-bodied parrots which have density estimates of less than 14 individuals/km^2 (Symes and Marsden 2007, Lee and Marsden 2012), and is higher than the density estimate of 13.6 parrots/km^2 for the Southern Mealy Amazon in tropical moist forest of South America (Lee and Marsden 2012). By comparison, high densities of 22.5- 29 parrots/km^2 are usually recorded for smaller parrot species (Marsden and Symes 2006). The unexpectedly high density of Northern Mealy Amazons in tropical moist forest of Los Chimalapas during the breeding season highlights the importance of the region for this threatened species. Therefore, large tracts of tropical moist forest such as Los Chimalapas may be biologically important not only for their high biodiversity (Peterson et al. 2003), but also because they support high densities of threatened species.

Notably, Northern Mealy Amazons were almost absent from Los Chimalapas during the non-breeding season, with such low encounter rates that it was not possible to model density estimates. Various studies have reported seasonal variation in abundance of psittacines (Renton 2002, Karubian et al. 2005, Lee and Marsden 2012), suggesting that parrots make seasonal movements among areas. Bjork (2004) also recorded a decline in relative abundance of the Northern Mealy Amazon during the non-breeding season in the Petén of Guatemala, and showed that Northern Mealy Amazons undertake migrations of 138 ± 61.9 km from the Petén in Guatemala to Campeche and Chiapas in Mexico. Therefore, it is highly likely that Northern Mealy Amazons in Los Chimalapas are undertaking similar long-distance migrations during the non-breeding season to potential alternative sites of El Ocote (80 km) or La Sepultura Biosphere Reserve (135 km) in Chiapas. Future research could apply radio-telemetry techniques (Bjork 2004) to identify alternate migration sites used by Northern Mealy Amazons in Mexico.

We also determined spatial variation in Northern Mealy Amazon density with a low density of parrots in secondary forest. Other studies have demonstrated lower parrot densities in human modified forests. Marsden and Pilgrim (2003) found lower densities of the Blue-eyed Cockatoo (*Cacatua ophthalmica*) in disturbed forests on Papua New Guinea, and Kinnaird et al. (2003) determined higher densities of the Seram Cockatoo (*Cacatua moluccensis*) in primary forests with high basal area and canopy closure. Similarly, Karubian et al. (2005) found that relative abundance of large macaws declined with increasing levels of human activity and landscape modification. These studies all relate to large parrot species, and along with the results obtained for the Northern Mealy Amazon, suggest that large threatened parrot species in particular may be more closely associated with primary forests.

Factors influencing selection of forest types by parrots

Northern Mealy Amazons in Los Chimalapas were more frequently recorded within 50 m of point counts in primary evergreen and riparian forests during the breeding season, and demonstrated selection for riparian forests, whereas parrots were rarely encountered in secondary forest, and used this forest type significantly less than expected. This corresponds with the findings of Bjork (2004) for the Northern Mealy Amazon in the Petén of Guatemala, who determined greater relative abundance of Northern Mealy Amazons in primary forest, whereas parrots were rarely observed perched in secondary forest. These results provide further support that the Northern Mealy Amazon is a primary forest specialist throughout its range in Mesoamerica.

Furthermore, the occurrence and number of parrots perched within a 50 m-radius of point counts was predicted by the density of large, tall trees around the point count. This is similar to studies in lowland Atlantic forest of Brazil where use of selectively logged forests by two Amazon parrot species was associated with large trees (Marsden et al. 2000). Legault et al. (2011) also found that presence of three parrot species in New Caledonia is related to canopy cover, where parrots selected areas with 80-100% canopy cover, avoiding areas with less than 20% canopy cover. Density of large trees was the main environmental variable influencing the abundance of avian species associated with primary tropical wet forest in Malaysia (Peh et al. 2005). Our results therefore indicate that during the breeding season Northern Mealy Amazons are strongly associated with primary forests where there is a greater density of canopy trees.

Comparison with Southern Mealy Amazon

The high seasonal fluctuation in abundance of Northern Mealy Amazons in Los Chimalapas, Mexico, corresponds with a similar seasonal fluctuation in abundance of Northern Mealy Amazons in the Petén of Guatemala (Bjork 2004). By comparison, Lee and Marsden (2012) recorded only slight seasonal variation in density of the Southern Mealy Amazon in floodplain forest of Southeast Peru. Therefore, it may be that the Northern Mealy Amazon in Mesoamerica exhibits greater seasonality in use of forest areas compared to the Southern Mealy Amazon in the Amazonian forests of South America.

Humid forests in Mesoamerica demonstrate marked seasonality in fruiting phenology, generally with peak fruit production during the dry season and in the transition from dry to wet season, while in South America the variation in fruiting phenology is less marked (Morellato et al. 2013). Given the high seasonality in fruit production of Central American forests, animal species that depend on these resources need to track fluctuations in resource abundance (Leighton and Leighton 1983, Fleming 1992). This could potentially lead seasonal movements by the Northern

Mealy Amazon in Central America, and Bjork (2004) determined that the seasonal decrease in abundance of Northern Mealy Amazons in Guatemala was associated with a corresponding decline in fruit production, suggesting that parrots make movements in search of food resources.

The Northern Mealy Amazon may also be facing greater pressures of forest loss resulting from anthropogenic activities compared to the Southern Mealy Amazon. In Mesoamerica, humid forests are becoming increasingly fragmented (Holzman 2008). Added to which, the Northern Mealy Amazon has large area requirements making seasonal movements over an area of 10,000 km^2 (Bjork 2004). The dependence of Northern Mealy Amazons on primary tropical moist forest, and their high seasonality in abundance and use of areas, emphasizes the need to conserve tracts of continuous primary tropical moist forest for the Northern Mealy Amazon in both breeding and migration areas.

Implications of tropical moist forest conversion

The results of our study demonstrate the importance of primary tropical moist forest, and in particular riparian forest, for the large-bodied Northern Mealy Amazon during the breeding season. Within the modified landscape of Los Chimalapas, secondary forest had distinct structural and floristic characteristics to primary forest, with a low density of smaller trees of lower tree and ramification height, indicative of trees of disturbed or regenerating forests (Torquebiau 1986). Secondary forests also had lower tree species richness and distinct species composition to that of primary evergreen and riparian forests. Hence, conversion of primary forest to secondary forest may have a negative effect on the status of Northern Mealy Amazon populations in the wild, as determined for the Carnaby's Cockatoo (*Zanda latirostris*) in the wheatbelt of Western Australia, which was unable to exploit dispersed food resources in fragmented landscapes resulting in eventual extirpation of the species (Saunders 1990).

Conversion of primary forest has occurred over recent decades in Los Chimalapas, where primary tropical moist forest comprised 77.6% (4651 km^2) of land cover at the end of the 1990s (Salas-Morales et al. 2001). However, by the year 2000, an additional 4.6% of lowland tropical moist forest was lost to land conversion, while open deforested areas increased by 5.3% in a decade, and there is currently a 5.8% annual rate of conversion of primary forest (Martínez-Pacheco 2012). This rate of land conversion is facilitated by the fact that most of Los Chimalapas represents community lands, with no legally protected areas, while a recent proposal for the area to be considered a Community Ecological Reserve was rejected by the Mexican government (Anaya and Álvarez 1994). Tropical moist forests have the greatest rate of biomass loss of all forest types in Mexico, presenting the highest increment in secondary forests (de Jong et al. 2010). This may be detrimental to Northern Mealy Amazon populations in the long-term as secondary forest had significantly lower densities of Northern Mealy Amazons, which used secondary forest less than expected by availability.

CONCLUSIONS

Understanding the requirements of large threatened parrot species such as the Northern Mealy Amazon is essential to develop appropriate strategies for forest management and conservation, and to assess the potential impact of anthropogenic activities on parrot populations in modified landscapes. Large-bodied, frugivorous, canopy species are among the avian species unlikely to persist in modified forests (Peh et al. 2005), however, almost nothing is known of the ecological requirements of the Northern Mealy Amazon in Mesoamerica. The results of our study in Mexico, and that of Bjork (2004) in Guatemala, both suggest that the Northern Mealy Amazon is a primary forest specialist that exhibits marked seasonality in use of forest areas. Therefore, the Northern Mealy Amazon in Central America may present important differences in ecological requirements from that of the Southern Mealy Amazon in South America. Northern Mealy Amazons are also under increased pressure from forest conversion and capture for the pet trade, making their populations especially vulnerable, and in need of immediate evaluation, and possible status reclassification.

Los Chimalapas in Mexico, and Petén in Guatemala, represent some of the largest tracts of primary tropical moist forest in Mesoamerica. However, both regions are suffering high rates of forest loss and conversion (Martínez-Pacheco 2012, Hodgdon et al. 2015), further limiting the availability of primary tropical moist forest for the Northern Mealy Amazon. As determined in our study, the increased conversion of primary tropical moist forest to secondary forest (de Jong et al. 2010) is likely to lead to reduced densities of large, threatened species such as the Northern Mealy Amazon. Brook et al. (2006) argue that afforestation via secondary forest succession may be a poor substitute for primary forest, particularly for the fraction of species that depend on primary old-growth forest, and do not persist in disturbed tropical forest (Peh et al. 2005). This makes it essential to implement strategies and incentives to conserve primary tropical moist forest in relatively undisturbed regions such as Los Chimalapas (Peterson and Navarro Sigüenza 2016), and reduce the rate of conversion to secondary forest, if we are to maintain populations of large forest-dependent species in the long-term.

ACKNOWLEDGMENTS

The study was conducted in partial fulfillment of a Ph.D. degree by MADLH at the Posgrado en Ciencias Biológicas, of the Universidad Nacional Autónoma de México (UNAM). Funding for the research was provided by the Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (UNAM-DGAPA-PAPIIT grant IN205716) to KR. MADLH received a Doctoral studies grant from the Consejo Nacional de Ciencia y Tecnología (Conacyt 215549). We are grateful to Idea Wild who provided field equipment, and to Patricia Escalante for logistical support. The Secretaria del Medio Ambiente y Recursos Naturales in Mexico provided research permits for the study. We are grateful to the authorities of the Santa María Chimalapa municipality for permission to work on their community lands, and to the local people of San Francisco La Paz, San Antonio Nuevo Paraíso and Chalchijapa who provided assistance in the field. We thank Marisela Martinez Ruiz for assistance in producing a map of the study site, Ruth Rodriguez Tejeda for advice on statistical analyses in R, and Alvaro Campos for assistance with taxonomic identification of tree species. We appreciate the constructive comments of the anonymous reviewers and subject editor which helped us to improve the manuscript.

LITERATURE CITED

Anaya, A. L., and M. Álvarez. 1994. *Plan de desarrollo y conservación de una reserva campesina en Los Chimalapas*. Instituto Nacional de Ecología, Mexico City, Mexico. [online] URL: http://www.inecc.gob.mx/descargas/publicaciones/28.pdf

Berkunsky, I., M. V. Simoy, R. E. Cepeda, C. Marinelli, F. P. Kacoliris, G. Daniele, A. Cortelezzi, J. Diáz, J. Mateo Friedman, and R. M. Aramburú. 2015. Assessing the use of forest islands by parrot species in a Neotropical savanna. *Avian Conservation and Ecology* 10(1):11. http://dx.doi.org/10.5751/ACE-00753-100111

BirdLife International. 2016*a*. BirdLife Data Zone. [online] URL: http//www.birdlife.org/datazone/index.html.

BirdLife International. 2016*b*. Species factsheet: *Amazona guatemalae*. [online] URL: http://www.birdlife.org.

Bjork, R. D. 2004. Delineating patterns and process in tropical lowlands: Mealy Parrot migration dynamics as a guide for regional conservation planning. Ph.D. Dissertation. Oregon State University. Scholars Archive, Oregon, USA. [online] URL: http://ir.library.oregonstate.edu/xmlui/handle/1957/10842

Brook, B. W., C. J. A. Bradshaw, L. P. Koh, and N. S. Sodhi. 2006. Momentum drives the crash: mass extinction in the tropics. *Biotropica* 38:302-305. http://dx.doi.org/10.1111/j.1744-7429.2006.00141.x

Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. *Introduction to distance sampling: estimating abundance of biological populations.* Oxford University Press, New York, New York, USA.

Bullock, S.H., and J.A. Solis-Magallanes. 1990. Phenology of canopy trees of a tropical deciduous forest in Mexico. *Biotropica* 22:22-35. http://dx.doi.org/10.2307/2388716

Burnham, K., and D. Anderson. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. Second Edition. Springer-Verlag, New York, New York, USA.

Byers, C. R., R. K. Steinhorst, and P. R. Krausman. 1984. Clarification of a technique for analysis of utilization-availability data. *Journal of Wildlife Management* 48:1050-1053. http://dx.doi.org/10.2307/3801467

Chapman, C. A., R. Wrangham, and L. J. Chapman. 1994. Indices of habitat-wide fruit abundance in tropical forests. *Biotropica* 26:160-171. http://dx.doi.org/10.2307/2388805

de Jong, B., C. Anaya, O. Masera, M. Olguín, F. Paz, J. Etchevers, R. D. Martínez, G. Guerrero, and C. Balbontín. 2010. Greenhouse gas emissions between 1993 and 2002 from land-use change and forestry in Mexico. *Forest Ecology and Management* 260:1689-1701. http://dx.doi.org/10.1016/j.foreco.2010.08.011

De Labra, M. A., P. Escalante, T. C. Monterrubio-Rico, and R. Coates-Estrada. 2010. Hábitat, abundancia y perspectivas de conservación de psitácidos en la reserva de Los Tuxtlas, Veracruz, México. *Ornitologia Neotropical* 21:599-610.

del Hoyo, J., and N. J. Collar. 2014. *Illustrated checklist of the birds of the world. Volume 1.* Lynx Editions, Barcelona, Spain.

Evans, B. E., J. Ashley, and S. J. Marsden. 2005. Abundance, habitat use, and movements of Blue-winged Macaws (*Primolius maracana*) and other parrots in and around an Atlantic Forest Reserve. *Wilson Bulletin* 117:154-164. http://dx.doi.org/10.1676/04-026

Fleming, T. H. 1992. How do fruit- and nectar-feeding birds and mammals track their food resources? Pages 355-391 *in* M. D. Hunter, T. Ohgushi, and P. W. Price, editors. *Effects of resource distribution on animal-plant interactions*. Academic Press, San Diego, California, USA.

Forshaw, J. M. 1989. *Parrots of the world*. Lansdowne Editions, Australia.

Greenberg, R. 1981. The abundance and seasonality of forest canopy birds on Barro Colorado Island, Panama. *Biotropica* 13:241-251. http://dx.doi.org/10.2307/2387802

Hastie, T., and R. Tibshirani. 1986. Generalized Additive Models. *Statistical Science* 1:297-310. http://www.jstor.org/stable/2245459

Hodgdon, B. D., D. Hughell, V. H. Ramos, and R. B. McNab. 2015. *2000-2013 deforestation trends in the Maya Biosphere Reserve, Guatemala*. Rainforest Alliance. [online] URL: http://www.rainforest-alliance.org/sites/default/files/publication/pdf/MBR-Deforestation_150213-2.pdf.

Holzman, B. A. 2008. *Tropical forest biomes*. Greenwood Press, London, UK.

INEGI. 2012. Carta hidrogeológica. Istmo de Tehuantepec, Oaxaca. Escala: 1, 250 000, México. Instituto Nacional de Estadística, Geografía e Informática. Mexico City, Mexico.

Karubian, J., J. Fabara, D. Yunes, J. P. Jorgenson, D. Romo, and T. B. Smith. 2005. Temporal and spatial patterns of macaw abundance in the Ecuadorian Amazon. *Condor* 107:617-626. http://dx.doi.org/10.1650/0010-5422(2005)107[0617:TASPOM]2.0.CO;2

Kinnaird, M. F., T. G. O´Brien, F. R. Lambert, and D. Purmiasa. 2003. Density and distribution of the endemic Seram Cockatoo *Cacatua moluccensis* in relation to land use patterns. *Biological Conservation* 109:227-235. http://dx.doi.org/10.1016/S0006-3207(02)00150-7

Krebs, C. J. 1999. *Ecological methodology*. Second Edition. Addison-Welsey Educational Publishers Inc., Menlo Park, California, USA.

Lawton, J. H., D. E. Bignell, B. Bolton, G. F. Bloemers, P. Eggleton, P. M. Hammond, M. Hodda, R. D. Holt, T. B. Larsen, N. A. Mawdsley, N. E. Stork, D. S. Srivastava, and A. D. Watt. 1998. Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* 391:72-76. http://dx.doi.org/doi:10.1038/34166

Lee, A. T. K., D. J. Brightsmith, M. P. Vargas, K. Q. Leon, A. J. Mejia, and S. J. Marsden. 2014. Diet and geophagy across a western Amazonian parrot assemblage. *Biotropica* 46:322-330. http://dx.doi.org/10.1111/btp.12099

Lee, A. T. K., and S. T. Marsden. 2012. The influence of habitat, season, and detectability on abundance across an Amazonia parrot assemblage. *Biotropica* 44:537-544. http://dx.doi.org/10.1111/j.1744-7429.2011.00847.x

Legault, A., V. Chartendraul, J. Theuerkauf , S. Rouys, and N. Barré. 2011. Large-scale habitat selection by parrots in New Caledonia. *Journal of Ornithology* 152:409-419. http://dx.doi.org/10.1007/s10336-010-0602-0

Leighton, M., and D. R. Leighton. 1983. Vertebrate responses to fruiting seasonality within a Bornean rain forest. Pages 181-196 *in* T. C. Whitmore, and A. C. Chadwick, editors. *Tropical rainforest: ecology and management*. Blackwell Scientific Press, Oxford, UK.

Loiselle, B.A. 1988. Bird abundance and seasonality in a Costa Rican lowland rainforest canopy. *Condor* 90: 761-772. http://dx.doi.org/10.2307/1368833

MacGregor-Fors, I., and M. E. Payton. 2013. Contrasting diversity values: statistical inferences based on overlapping confidence intervals. *PLoS One* 8:e56794. http://dx.doi.org/10.1371/journal.pone.0056794

Marques, T. A., L. Thomas, S. G. Fancy, and S. T. Buckland. 2007. Improving estimates of bird density using multiple-covariate distance sampling. *Auk* 124:1229-1243. http://dx.doi.org/10.1642/0004-8038(2007)124[1229:IEOBDU]2.0.CO;2

Marsden, S. J. 1992. The distribution, abundance and habitat preferences of the Salmon-crested Cockatoo *Cacatua moluccensis* on Seram, Indonesia. *Bird Conservation International* 2:7-14. http://dx.doi.org/10.1017/S0959270900000435

Marsden, S. J. 1999. Estimation of parrot and hornbill densities using a point count distance sampling method. *Ibis* 141:377-390. http://dx.doi.org/10.1111/j.1474-919X.1999.tb04405.x

Marsden, S. J., and J. D. Pilgrim. 2003. Factors influencing the abundance of parrots and hornbills in pristine and disturbed forests on New Britain. *Ibis* 145:45-53. http://dx.doi.org/145:45–53. 10.1046/j.1474-919X.2003.00107.x

Marsden, S. J., and K. Royle. 2015. Abundance and abundance change in the world´s parrots. *Ibis* 157:219-229. http://dx.doi.org/doi: 10.1111/ibi.12236

Marsden, S. J., and C. T. Symes. 2006. Abundance and habitat associations of parrots at a hillforest site in Papua New Guinea. *Pacific Conservation Biology* 12:15-21. http://dx.doi.org/10.1071/PC060015

Marsden, S. J., M. Whiffin, L. Sadgrove, and P. Guimarães Jr. 2000. Parrot populations and habitat use in and around two lowland Atlantic forest reserves, Brazil. *Biological Conservation* 96:209-217. http://dx.doi.org/10.1016/S0006-3207(00)00071-9

Martínez-Pacheco, A. I. 2012. Monitoreo del cambio de uso de suelo en Los Chimalapas 2000-2003. Pages 86-94 *in* D. Ortega del Valle, T. Carranza-López, and J. Martínez-Pérez, editors. *Una mirada desde el corazón de la jícara de oro. Experiencias de conservación en la Selva Zoque de Los Chimalapas*. WWF-México, Oaxaca, Mexico.

Morellato, L. P. C., M. G. Camargo, and E. Gressler. 2013. A review of plant phenology in South and Central America. Pages 91-113 *in* M. D. Schwarts, editor. *Phenology: an interactive environmental science*. Second Edition. Springer, New York, New York, USA.

Navarro-Sigüenza, A. G., L. C. Márquez, and H. O. Monroy. 2008. Vertebrados terrestres de Los Chimalapas: una prioridad de conservación. CONABIO. *Biodiversitas* 77:10–15. [online] URL: http://www.biodiversidad.gob.mx/Biodiversitas/Articulos/biodiv77art3.pdf

Nue, A. W., C. R. Byers, and J. M. Peek. 1974. A technique for analysis of utilization-availability data. *Journal of Wildlife Management* 38:541–545. http://dx.doi.org/10.2307/3800887

Olah, G., S. H. M. Butchart, A. Symes, I. Medina Guzman, R. Cunningham, D. J. Brightsmith, and R. Heinsohn. 2016. Ecological and socio-economic factors affecting extinction risk in parrots. *Biodiversity and Conservation* 25:205-223. http://dx.doi.org/10.1007/s10531-015-1036-z

Olson, D. M., E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. N. Powell, E. C. Underwood, J. A. D'Amico, I. Itoua, H. E. Strand, J. C. Morrison, C. J. Loucks, T. F. Allnutt, T. H. Ricketts, Y. Kura, J. F. Lamoreux, W. W. Wettengel, P. Hedao, and K. R. Kassem. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. *BioScience* 51:933-938. http://dx.doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2

Payton, M. E., M. H. Greenstone, and N. Schenker. 2003. Overlapping confidence intervals or standard error intervals: what do they mean in terms of statistical significance? *Journal of Insect Science* 3:1-6. http://dx.doi.org/10.1673/031.003.3401

Peh, K. S.-H., J. de Jong, N. S. Sodhi, S. L,-H Lim, and C. A.-M. Yap. 2005. Lowland rainforest avifauna and human disturbance: persistence of primary forest birds in selectively logged forests and mixed-rural habitats of southern Peninsular Malaysia. *Biological Conservation* 123:489-505. http://dx.doi.org/10.1016/j.biocon.2005.01.010

Pennington, T. D., and J. Sarukhán. 1998. *Arboles tropicales de México*. Second Edition. Fondo de Cultura Económica, Mexico City, Mexico.

Peterson, A. T., and A. G. Navarro-Sigüenza. 2016. Bird conservation and biodiversity research in Mexico: status and priorities. *Journal of Field Ornithology* 87:121-132. http://dx.doi.org/10.1111/jofo.12146/abstract

Peterson, A. T., A. G. Navarro-Sigüenza, B. E. Hernández-Baños, G. Escalona-Segura, F. Rebon-Gallardo, E. Rodríguez-Ayala, E. M. Figueroa-Esquivel, and L. Cabrera-García. 2003. The Chimalapas region, Oaxaca, Mexico: a high-priority region for bird conservation in

Mesoamerica. *Bird Conservation International* 13:227-253. http://dx.doi.org/10.1017/S0959270903003186

QGIS Development Team 2015. QGIS Geographic Information System. Open Source Geospatial Foundation Project. [online] URL: http://www.qgis.org/

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [online] URL: http://www.R-project.org/.

Renton, K. 2002. Seasonal variation in occurrence of macaws along a rainforest river. *Journal of Field Ornithology* 73:15-19. http://dx.doi.org/10.1648/0273-8570-73.1.15

Ríos-Muñoz, C. A., and A. G. Navarro-Sigüenza. 2009. Efectos del cambio de uso del suelo en la disponibilidad hipotética de hábitat para los psitácidos de México. *Ornitologia Neotropical* 20:491-509.

Salas-Morales, S. H., L. Schibli, and E. Torres-Bahena. 2001. La importancia ecológica y biológica. Pages 29-41 *in* R. Aparicio Cid, editor. *Chimalapas. La última oportunidad*. WWF-México, Secretaría de Medio Ambiente, Recursos Naturales y Pesca, Mexico City, Mexico.

Saunders, D. A. 1990. Problems of survival in an extensively cultivated landscape: the case of Carnaby´s Cockatoo *Calyptorhynchus funereus latirostris*. *Biological Conservation* 54:277-290. http://dx.doi.org/10.1016/0006-3207(90)90057-V

Şekercioğlu, C. H., G. C. Daily, and P. R. Ehrlich. 2004. Ecosystem consequences of bird declines. *Proceedings of the National Academy of Sciences USA* 101:18042-18047. http://dx.doi.org/10.1073/pnas.0408049101

Skole, D., and C. Tucker. 1993. Tropical deforestation and habitat fragmentation in the Amazon: satellite data from 1978 to 1988. *Science* 260:1905-1910. http://dx.doi.org/10.1126/science.260.5116.1905

Snyder, N., P. McGowan, J. Gilardi, and A. Grajal (editors). 2000. *Parrots. Status survey and conservation action plan 2000-2004*. IUCN, Gland, Switzerland and Cambridge, UK.

Symes, C. T., and S. J. Marsden. 2007. Patterns of supra-canopy flight by pigeons and parrots at a hill-forest site in Papua New Guinea. *Emu* 107:115-125. http://dx.doi.org/10.1071/MU06041

Thomas L, J. L. Laake, S. Strindberg, F. F. C. Marques, S. T. Buckland, D. L. Borchers, D. R. Anderson, K. P. Burnham, S. L. Hedley, J. H. Pollard, and J. R. B. Bishop. 2006. Distance 6.0. Release 2. University of St. Andrews, UK. [online] URL:http://www.ruwpa.st-and.ac.uk/distance/

Torquebiau, E. F. 1986 Mosaic patterns in Dipterocarp rain forest in Indonesia, and their implications for practical forestry. *Journal of Tropical Ecology* 2:301-325. http://www.jstor.org/stable/2559460

Torres Colín, R. 2004. Tipos de vegetación. Pages 105-117 *in* A. J. García-Mendoza, M. J. Ordoñez, and M. Briones-Salas, editors. *Biodiversidad de Oaxaca*. Instituto de Biología, UNAM, Fondo Oaxaqueño para la Conservación de la Naturaleza, WWF-México, Mexico City, Mexico.

Trejo, I. 2004. Clima. Pages 67-85 *in* A. J. García-Mendoza, M. J. Ordoñez, and M. Briones-Salas, editors. *Biodiversidad de Oaxaca*. Instituto de Biología, UNAM, Fondo Oaxaqueño para la Conservación de la Naturaleza, WWF-México, Mexico City, Mexico.

Vázquez Torres, M., S. Armenta Montero, J. Campos Jiménez, and C. I. Carvajal Hernández. 2010. *Árboles de la región de Los Tuxtlas*. Secretaria de Educación-Gobierno del Estado de Veracruz, Xalapa, Veracruz, Mexico.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. *Science* 277:494-499. http://dx.doi.org/10.1126/science.277.5325.494

Wenner, T. J., M. A. Russello, and T. F. Wright. 2012. Cryptic species in a Neotropical parrot: genetic variation within the *Amazona farinosa* species complex and its conservation implications. *Conservation Genetics* 13:1427-1432. http://dx.doi.org/10.1007/s10592-012-0364-8

Wood, S. N. 2006. *Generalized Additive Models: an introduction with R*. Chapman and Hall/CRC Press, Florida, USA

Wood, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society B* 73:3-36. http://dx.doi.org/10.1111/j.1467-9868.2010.00749.x

Wright, S. J., and H. C. Muller-Landau. 2006*a*. The future of tropical forest species. *Biotropica* 38:287-301. http://www.jstor.org/stable/30043245

Wright, S. J., and H. C. Muller-Landau. 2006*b*. The uncertain future of tropical forest species. *Biotropica* 38:443-445. http://dx.doi.org/10.1111/j.1744-7429.2006.00177.x

Zar, J. H. 1999. *Biostatistical analysis*. Fourth Edition. Prentice Hall Inc, New Jersey, USA.

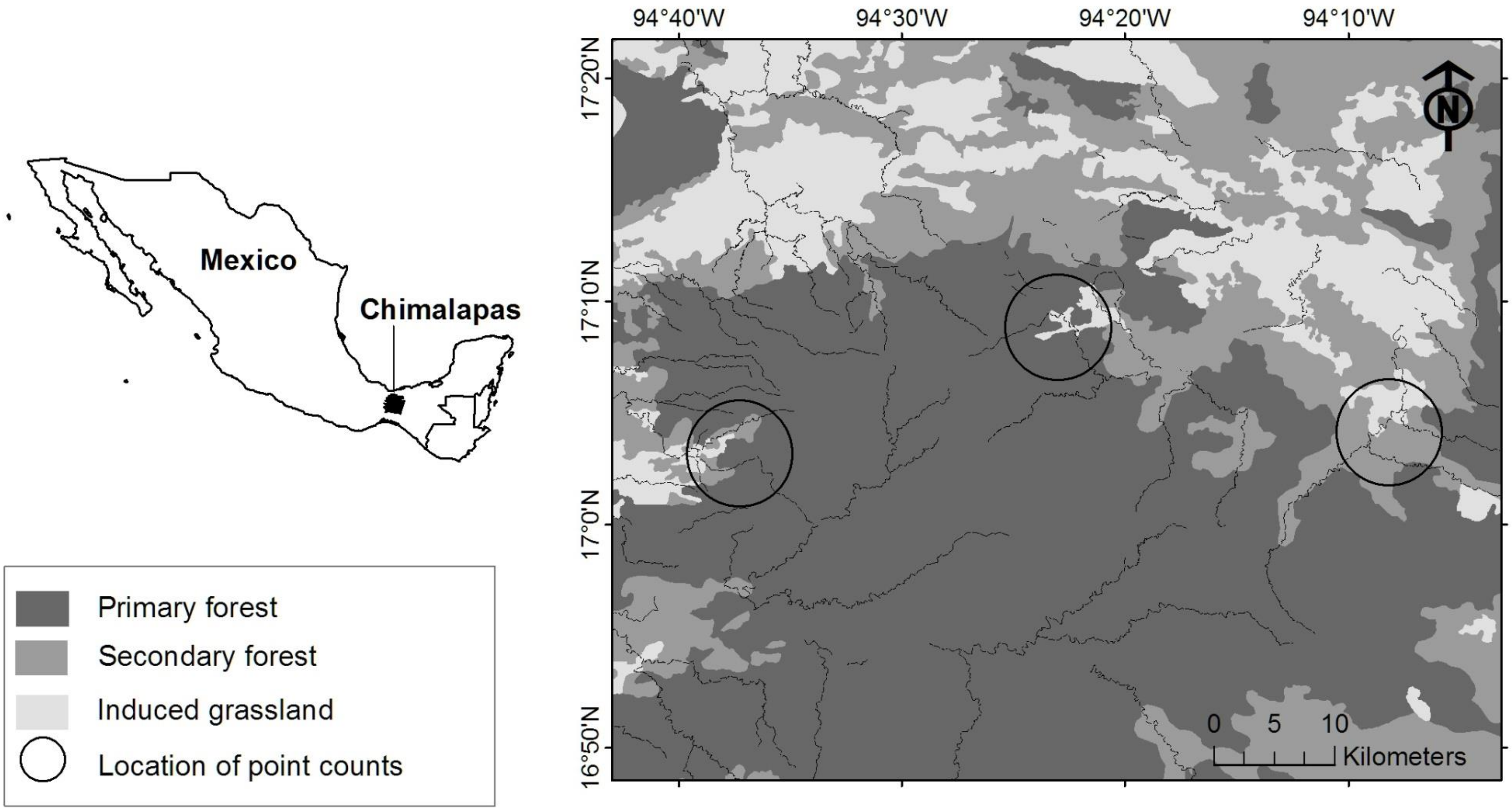
Figure legends

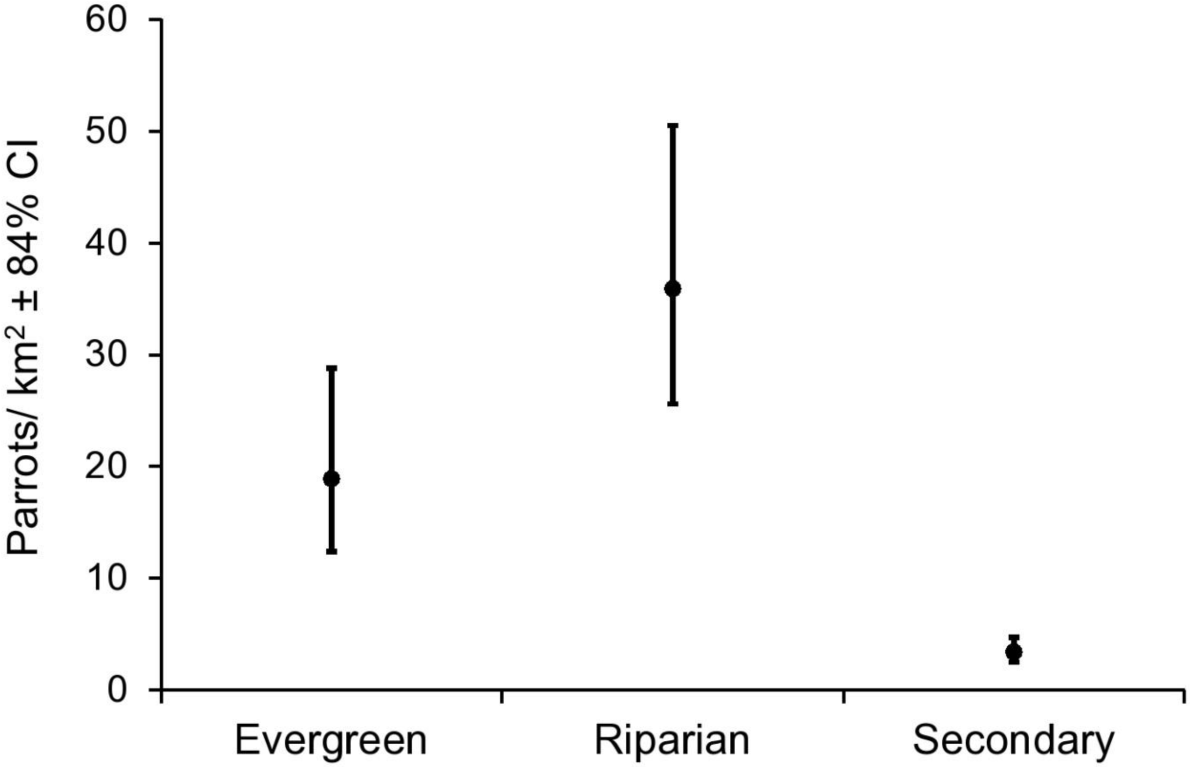
Fig. 1. The study area in northern Chimalapas, Mexico, showing the modified tropical moist forest landscape, main rivers (dark lines), and the general location of point counts.

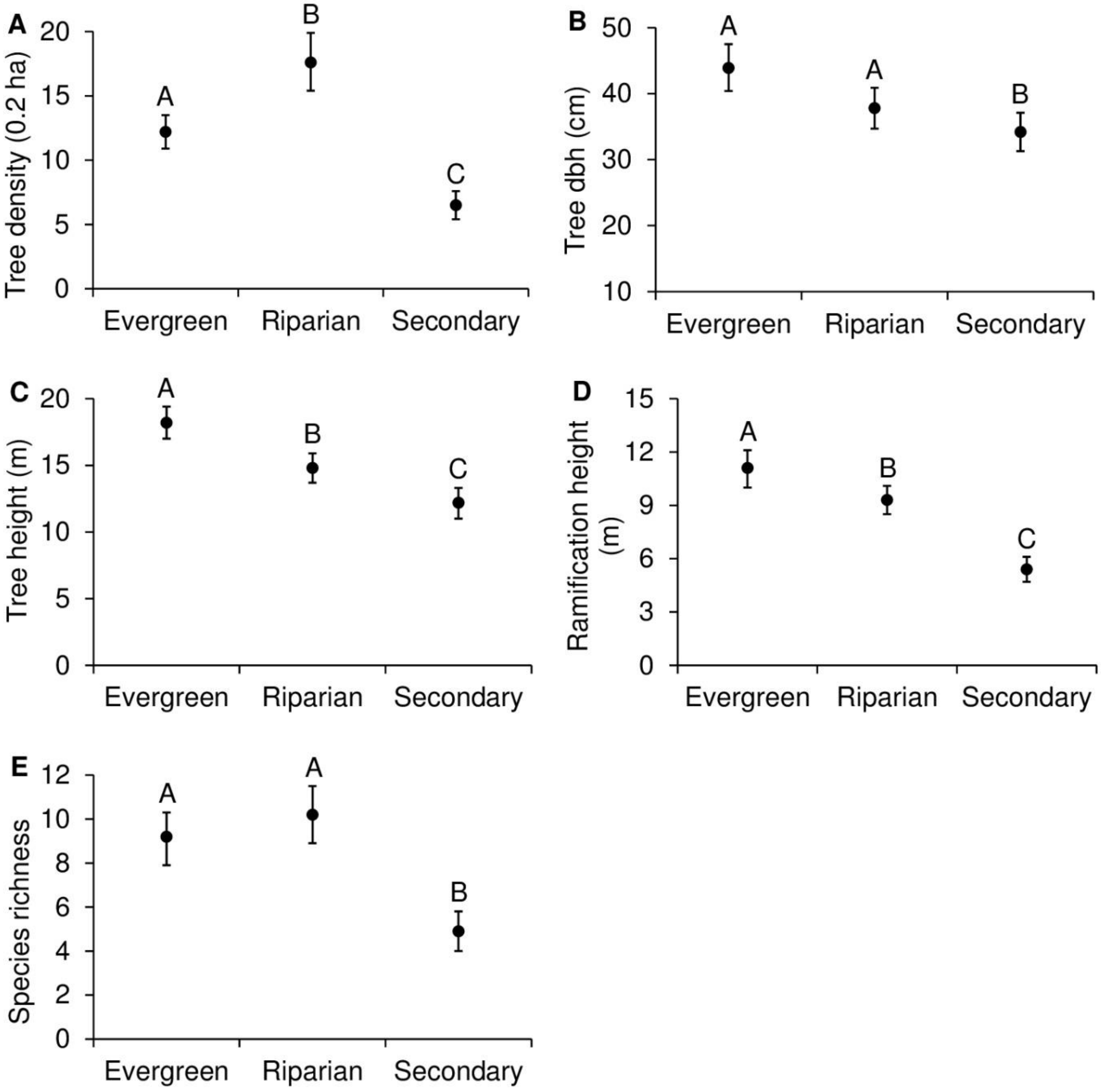
Fig. 2. Northern Mealy Amazon density estimates with 84% confidence intervals in evergreen, riparian, and secondary tropical moist forest in Los Chimalapas, Mexico, during the breeding season of March 2014.

Fig. 3. Variation among forest types in metrics of trees (≥10 cm dbh) within a 25 m-radius of point counts for A) tree density in 0.2 ha, B) tree diameter at breast height (cm), C) total tree height (m), D) ramification height to the first major branch (m), and E) tree species richness, in tropical moist forest of Los Chimalapas, Mexico. Mean values per point count with 95% confidence intervals are shown. Letters indicate significantly different Dunn posthoc pairwise comparisons among forest types.

Fig. 4. Proportional abundance of tree species within a 25 m-radius of point counts in A) evergreen, B) riparian, and C) secondary tropical moist forest in Los Chimalapas, Mexico. Only tree species contributing >5% of tree abundance in each forest type are shown.


Mexico
Chimalapas
Primary forest
Secondary forest
Induced grassland
Location of point counts
94°40'W
94°30'W
94°20'W
94°10'W
17°20'N
17°10'N
17°0'N
16°50'N
N
0
5
10
Kilometers


60
50
40
30
20
10
0
Parrots/ km^2 ± 84% CI
Evergreen
Riparian
Secondary


A
Tree density (0.2 ha)
0
5
10
15
20
Evergreen
Riparian
Secondary
A
B
C
B
Tree dbh (cm)
10
20
30
40
50
Evergreen
Riparian
Secondary
A
A
B
C
Tree height (m)
0
5
10
15
20
Evergreen
Riparian
Secondary
A
B
C
D
Ramification height (m)
0
3
6
9
12
15
Evergreen
Riparian
Secondary
A
B
C
E
Species richness
0
2
4
6
8
10
12
Evergreen
Riparian
Secondary
A
A
B

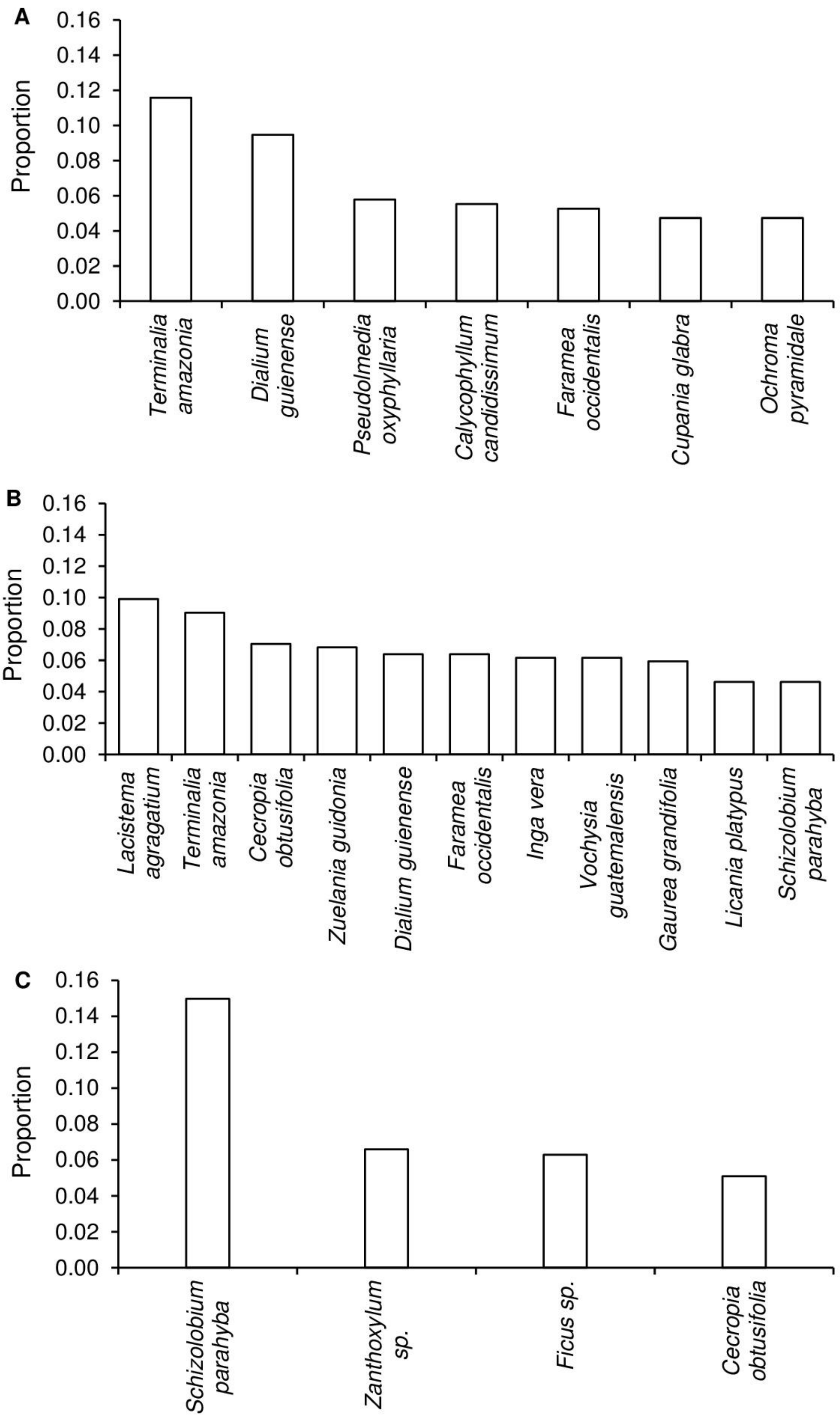

A
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
Proportion
Terminalia amazonia
Dialium guienense
Pseudolmedia oxyphyllaria
Calycophyllum candidissimum
Faramea occidentalis
Cupania glabra
Ochroma pyramidale
B
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
Proportion
Lacistema agragatium
Terminalia amazonia
Cecropia obtusifolia
Zuelania guidonia
Dialium guienense
Faramea occidentalis
Inga vera
Vochysia guatemalensis
Gaurea grandifolia
Licania platypus
Schizolobium parahyba
C
0.16
0.14
0.12
0.10
0.08
0.06
0.04
0.02
0.00
Proportion
Schizolobium parahyba
Zanthoxylum sp.
Ficus sp.
Cecropia obtusifolia

Table 1. Multiple-covariates Distance Sampling model parameters for density estimates to 84% confidence intervals of Northern Mealy Amazons during the breeding season (March 2014) in Los Chimalapas, Mexico.

Stratum	Number of point counts	Mean density (ind/km^2 ± SE)	Mean cluster size (ind ± SE)	Mean density of cluster (ind/km^2 ± SE)	Effective detection radius (m) ± SE
Global	120	19.5 ± 6.2	2.8 ± 0.2	6.3 ± 2.9	61.7 ± 4.7
Evergreen forest	33	18.9 ± 5.7	4 ± 0.5	4.7 ± 1.2	57.8 ± 5.5
Riparian forest	27	35.9 ± 8.7	2.8 ± 0.3	12.59 ± 2.6	55.5 ± 4.3
Secondary forest	60	3.4 ± 0.8	2.1 ± 0.2	1.5 ± 0.3	73.5 ± 5.3

Table 2. Principal Components Analysis of forest structure and floristic composition variables within a 25 m-radius of point counts in tropical moist forest of Los Chimalapas, Mexico ($r > 0.7$ marked in bold font).

	Component 1	Component 2	Component 3
Eigenvalue	3.7	1.9	1.2
% Explained	63.3	25.2	6.2
Correlations with individual variables			
Mean tree diameter at breast height	**0.93**	0.23	0.27
Tree density	0.12	**0.81**	0.16
Mean tree height	0.28	0.14	**0.71**
Mean ramification height	0.19	0.25	0.49
Species richness	0.07	0.44	0.36
Terminalia amazonia	0.04	0.06	-0.05
Dialium guianense	0.04	0.08	-0.05
Ficus sp.	(-)	(-)	0.06
Spondias mombin	(+)	-0.01	0.02
Ochroma pyramidale	(-)	(+)	-0.08
Sloanea meianthera	(-)	-0.03	0.02

Table 3. Proportional availability and use of three forest types by Northern Mealy Amazons, with Bonferroni confidence intervals, in tropical moist forest of Los Chimalapas, Mexico, during the breeding season of March 2014. * = $P < 0.05$

Habitat	Proportion available	Proportion used	Bonferroni confidence intervals
Evergreen forest	0.66	0.40	0.26 ≤ obs ≤ 0.55*
Riparian forest	0.19	0.54	0.39 ≤ obs ≤ 0.68*
Secondary forest	0.16	0.06	0.00 ≤ obs ≤ 0.13*

CAPITULO II

(Aceptado para su publicación en *Tropical Conservation Science*)

Importance of large, old primary forest trees in nest-site selection by the Northern Mealy Amazon (*Amazona guatemalae*)

Short title: Nest-site selection by the Northern Mealy Amazon

Miguel Ángel De Labra-Hernández[1] and Katherine Renton[2]*

[1]Posgrado en Ciencias Biológicas, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico.

[2]Estación de Biología Chamela, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 21, San Patricio-Melaque, Jalisco, Mexico.

*Corresponding Author: K. Renton (krenton@ib.unam.mx)

Telephone & Fax: 52-315-3510202

Estado del proceso: *En prensa*

Abstract

The increasing conversion of primary tropical moist forest to secondary forest may have consequences for threatened, large-bodied cavity-nesters, such as the Northern Mealy Amazon (*Amazona guatemalae*). We determined availability and characteristics of tree-cavities in 24 1-ha survey plots in Los Chimalapas, southeast Mexico, with 9 plots in evergreen forest, 7 in riparian, and 8 in secondary forest. We compared these with 40 parrot nest-trees to determine whether parrots select cavities with specific characteristics for nesting. Over half of Northern Mealy Amazon nests occurred in live trees of *Terminalia amazonia* (32.5%), and *Dialium guianense* (20%). Compared to available cavities, the Northern Mealy Amazon selected nest-cavities in significantly larger trees, at a greater height above the ground, with larger internal diameter, and greater depth. In particular, internal diameter and cavity depth predicted whether a cavity was selected as a nest-site by parrots. We found a low density of 2.3 available cavities/ha in the study site, although only 1.6 cavities/ha had characteristics suitable for use as nest-sites by parrots. Cavities in secondary forest occurred in smaller trees, at a lower height, and with shallower depth, where only 0.75 cavities/ha were suitable for nesting by parrots. Our results demonstrate that the Northern Mealy Amazon requires nest-cavities in large, old trees able to form large cavities, the majority of which occur in primary forest. The low density of suitable nest-sites for parrots in secondary forest suggests that increased degradation of primary tropical moist forest may have long-term implications for reproduction of this threatened species.

Keywords: Los Chimalapas, Psittaciformes, resource use and availability, secondary cavity-nesters, tree-cavity characteristics, tropical moist forest

Introduction

A large proportion of threatened avian species are secondary cavity-nesters that do not construct their own nest-cavities, but depend on the availability of existing cavities (Monterrubio-Rico & Escalante-Pliego, 2006; Newton, 1994). Tropical moist forests are reported to have a high density of tree-cavities (Boyle, Ganong, Clark, & Hast, 2008), and support a variety of cavity-nesting bird species (Monterrubio-Rico & Escalante-Pliego, 2006). However, not all cavities have characteristics suitable for use as nest-sites by birds (Cockle, Martin, & Drever, 2010; Politi, Hunter, & Rivera, 2010; Vázquez & Renton, 2015), and there may be a low density of tree-cavities suitable for large-bodied secondary cavity-nesters (de la Parra-Martínez, Renton, Salinas-Melgoza, & Muñoz-Lacy, 2015). Secondary cavity-nesting birds may also select tree-cavities with specific characteristics of height from the ground, entrance diameter, and cavity depth (Cockle, Martin, & Wiebe, 2011; Politi, Hunter, & Rivera, 2009), which could restrict access by predators increasing the likelihood of nest success (Cockle, Bodrati, Lammertink, & Martin, 2015). Furthermore, tropical moist forests are increasingly being converted to secondary forests, having a high biomass loss of primary forest, and the highest increment rate of secondary forest (de Jong et al., 2010). This may have consequences for secondary cavity-nesting birds as human-managed forests have been found to have a lower availability of tree-cavities for use by birds (Cockle, Martin, & Drever, 2010; Politi, Hunter, & Rivera, 2010).

The majority of Psittaciformes (parrots) are secondary cavity-nesters, where medium to large-bodied species use tree-cavity nesting substrates (Renton, Salinas-Melgoza, De Labra-Hernández, & de la Parra-Martínez, 2015). The greatest diversity of tree-cavity nesting Psittaciformes occurs in the Neotropics, almost half of which are considered internationally threatened (Renton, Salinas-Melgoza, De Labra-Hernández, & de la Parra-Martínez, 2015), with the greatest number and proportion of threatened parrot species worldwide occurring in the Neotropics (Olah et al., 2016). Only a few studies have evaluated nest-site availability and selection by Psittaciformes, and these demonstrate that parrots select nest-sites in large trees, based on cavity characteristics of height from the ground, entrance diameter, and cavity depth (Brightsmith & Bravo, 2006; de la Parra-Martínez, Renton, Salinas-Melgoza, & Muñoz-Lacy, 2015; Enkerlin-Hoeflich, 1995; Snyder, Wiley, & Kepler, 1987; Stojanovic, Webb, Roshier, Saunders, & Heinsohn, 2012) . Furthermore, many parrots are large-bodied secondary cavity-nesters that may be limited by the availability of tree-cavities with suitable dimensions for nesting (de la Parra-Martínez, Renton, Salinas-Melgoza, & Muñoz-Lacy, 2015).

The Northern Mealy Amazon (*Amazona guatemalae*) is the largest Amazon parrot in continental America (Forshaw, 1989), and inhabits tropical moist forests of Mesoamerica (Bjork, 2004). The species is internationally considered Near Threatened (BirdLife International, 2016), and has recently been split from the more widely distributed Southern Mealy Amazon (*Amazona farinosa*) in South America (Wenner, Russello, & Wright, 2012). However, almost nothing is known of the species' nesting requirements, or how this may be affected by the increasing conversion of tropical moist forest to secondary forests. Only one study in the Petén of Guatemala determined that the

Northern Mealy Amazon uses nest-sites in large trees of 22 species (Bjork, 2004). Therefore, in the present study we aimed to determine nest-site requirements of the Northern Mealy Amazon, and the availability of tree-cavities for use by parrots in primary and secondary tropical moist forest. We further aimed to determine whether parrots select cavities based on their characteristics for use as nest-sites, and evaluate the consequences of primary forest conversion for nest-site availability and selection by the Northern Mealy Amazon.

Methods

Study area

We conducted the study in a 56 km^2 region of Los Chimalapas in northeastern Oaxaca, Mexico, comprising three main areas of Chalchijapa (17° 03' 15''N; 94° 39' 23''W), San Antonio Nuevo Paraíso (17° 09' 38''N; 94° 21' 9''W), and La Fortaleza (17° 09' 32.2''N; 94° 13' 45.3''W) within the municipality of Santa Maria Chimalapa. Mean annual temperature in the region is 22–26°C, with high annual rainfall of 2,000–4,500 mm, presenting a short dry season from March to June (Trejo, 2004). The dominant vegetation in the region is tropical moist forest comprised of primary evergreen forest that covers 45.7% of the landscape (Martínez-Pacheco, 2012), with common tree species of *Dialium guianense*, *Terminalia amazonia*, *Brosimum alicastrum* and *Cojoba arborea* (Rzedowski, 2006; Torres Colín, 2004). Riparian forest occurs along permanent rivers, with common tree species of *Ficus* sp., *Garcinia macrophylla*, *Vochysia guatemalensis* and *Inga vera* (Torres Colín, 2004). Nevertheless, in Santa Maria Chimalapa over the last few decades a total of 2,046.8 km^2 of primary tropical evergreen forest has been degraded, with a current rate of loss of 5.8% of primary forest per year (Martínez-Pacheco, 2012), mainly due to increased cattle-grazing and selective logging. This contrasts with the 6.8% increase in secondary forest recorded in the region from 2000-2003 (Martínez-Pacheco, 2012). Research permits for the study were provided by the Secretaria del Medio Ambiente y Recursos Naturales in Mexico.

Nest-site characteristics

We located nests of the Northern Mealy Amazon during the months of February to May over four consecutive breeding seasons in 2013-2016, by observation of the behavior of nesting pairs, and with the assistance of local guides. We used single-rope tree-ascending techniques (Houle, Chapman, & Vickery, 2004; Perry & Williams, 1981) to confirm nesting activity by the presence of eggs or chicks in the nest, and take measurements of the nest cavity. For each nest-tree located, we recorded tree species, diameter at breast height (dbh), condition (live or dead), and GPS location. We also noted cavity origin as formed by decay processes (decayed) or excavated by primary cavity nesters (Aitken & Martin, 2007). Finally, we measured cavity characteristics of height from the ground, entrance width and length, cavity depth, internal diameter, and diameter of the supporting structure (trunk or branch) where the cavity was located (Cockle, Martin, & Wiebe, 2008).

We located a total of 48 Northern Mealy Amazon nests in 40 distinct nest-trees, where 8 nest-trees were reused by parrots between seasons. However, we considered only individual nest-trees as the nest-site for all analyses. Of the 40 nest-trees, 11 occurred in primary forest (evergreen = 9 nest-trees, riparian = 2 nest-trees), with an additional 17 nest-sites located in remnant trees in areas cleared for cattle grazing at the edge of primary forest, and 12 nest-trees occurred in secondary forest.

Cavity availability

To determine the availability of tree-cavities in tropical moist forest we established 24 1-ha survey plots (100 x 100 m) distributed among the three study areas, with 9 tree-cavity survey plots in evergreen forest, 7 in riparian, and 8 in secondary forest. In each survey plot, we conducted an intensive search for cavities inspecting all trees with 10 x 40 binoculars. On locating a tree-cavity, we measured the same variables as for the parrot nests. We used a 15-m extendible tree-measuring pole to measure cavity height from the ground and entrance length. A 50 cm length, horizontal plastic tube, with 1 cm graduated markings, was attached to the top of the tree-measuring pole to measure cavity entrance width and internal diameter. Finally, we used a weighted fishing-line that passed through the top of the tree-measuring pole to determine cavity depth by the length the line descended within the cavity (Vázquez & Renton, 2015). This enabled us to measure the dimensions of the majority of cavities, however for 10 cavities >16 m above the ground we used a digital dendrometer (Criterion RD 1000) to estimate cavity height, entrance width and length, and support diameter (Cockle, Martin, & Drever, 2010), but were unable to measure internal diameter and depth of these cavities.

To be comparable with other studies of tree-cavity availability in tropical forests, we measured all tree-cavities with ≥2 cm entrance diameter and ≥8 cm cavity depth (Cockle, Martin, & Wiebe, 2008). However, we defined a cavity as available for use by parrots based on measurements (Saunders, Smith, & Rowley, 1982) of 5 specimens of the Northern Mealy Amazon collected in Mexico, and located in the National Bird Collection of the Institute of Biology at Universidad Nacional Autónoma de Mexico in Mexico City. These Northern Mealy Amazon specimens had a mean diameter at the widest point (shoulder-to-shoulder) of 10.2 ± 1.2 cm (range 8.9–11.5 cm, n = 5), with a breast-to-back measurement of mean 7.5 ± 0.2 cm (range 7.3–7.8 cm, n = 5). Therefore, it is unlikely that Northern Mealy Amazons could enter a cavity with an entrance diameter less than 7 cm, and we considered as available to parrots only cavities with ≥7.0 cm entrance diameter. We also estimated the density of cavities suitable for nesting by Northern Mealy Amazons considering the minimum characteristics of cavities used as nest-sites by parrots.

Statistical analyses

Although we measured all tree-cavities found in survey plots, we conducted statistical analysis only on cavities accessible to parrots (entrance diameter ≥7 cm) that were considered as available for parrots. Kolmogorov-Smirnov analysis of normality determined that data on tree dbh, cavity height above the ground, entrance width and internal diameter had a normal distribution. Therefore, we applied one-way ANOVA to compare these characteristics of available cavities among the three vegetation types of evergreen, riparian and secondary forest. Data on number of available cavities in each survey plot, cavity entrance length, cavity depth, and support diameter did not present a normal distribution; therefore, we applied Kruskal-Wallis ANOVAs to compare these characteristics of available cavities among vegetation types. We conducted Tukey post-hoc analyses for one-way ANOVAs and Dunn post-hoc analyses for Kruskal-Wallis ANOVAs (Zar, 1999).

We calculated the standardized Levins' (1968) niche breadth index for tree species used as nest-sites by Northern Mealy Amazons, where a value close to 0 indicates that nesting is concentrated on only a few tree species, whereas a value close to 1 indicates a broad use of tree species as nest-sites (Colwell & Futuyma, 1971). We also applied G-test to determine whether use of tree species as nest-sites by the Northern Mealy Amazon corresponded to the availability of accessible cavities in each tree species. Finally, we generated simultaneous confidence intervals with Bonferroni adjusted alpha for the proportional use of each tree species as a nest-site (Byers, Steinhorst, & Krausman, 1984; Nue, Byers, & Peek, 1974). Use of a tree species as a nest-site is considered significantly different when the expected proportion of use based on availability falls outside the confidence interval of observed use (Byers, Steinhorst, & Krausman, 1984).

We first compared characteristics of Northern Mealy Amazon nest-sites among vegetation types in the modified landscape using one-way ANOVAs with Tukey post-hoc comparisons for nest-tree dbh, entrance length, cavity depth, internal diameter, and support diameter, and applied Kruskal-Wallis ANOVAs with Dunn post-hoc comparisons for cavity height and entrance width. We determined no significant differences in nest-site characteristics, therefore combined nest-site data in comparisons with available cavities. Combined data did not present a normal distribution, therefore to determine whether Northern Mealy Amazons selected nest-sites based on cavity characteristics we used Mann-Whitney U test to compare characteristics of cavities used as nests by parrots with those of all available cavities (entrance diameter ≥7.0 cm) recorded in survey plots.

Finally, we applied multiple logistic regression to determine whether cavity characteristics predicted use of a cavity as a nest-site by Northern Mealy Amazons (nest = 1, available cavity = 0). As cavity entrance diameter would limit access by parrots and potential predators we considered the smallest entrance dimension (length or width) for multiple logistic regression, although in 95% of cases the smallest diameter was entrance width. Support diameter was strongly correlated with internal cavity diameter ($r = 0.82$, $P < 0.001$), therefore we excluded the variable of support diameter from the initial logistic regression model. We used the Wald statistic (Quinn & Keough, 2002) to determine which variable (tree dbh, cavity height, smallest entrance diameter, cavity depth, and internal cavity diameter) predicted selection of a cavity as a nest-site by the Northern Mealy Amazon. We also evaluated the odds ratio and the inflection point of the probability curve for significant variables to determine the value above which there is a greater than 50% probability that a cavity would be selected as a nest-site by parrots. Descriptive statistics are presented as mean values with standard deviation, and we considered a value of $P = 0.05$ as significantly different for statistical analyses.

Results

Nest-site characteristics

The 40 Northern Mealy Amazon nest-trees comprised 13 tree species (Figure 1), although parrots exhibited a narrow 0.39 niche-breadth of tree species used for nesting with over half of all Northern Mealy Amazon nest-sites occurring in live trees of *Terminalia amazonia* (32.5%; n = 13 nest-trees), and *Dialium guianense* (20%; n = 8 nest-trees). The majority of nest-sites occurred in cavities in live trees (75%; n = 30), located either on the main trunk or secondary branch (50%; n = 20 in both cases), and all were formed by decay processes. Overall, Northern Mealy Amazon nest-sites occurred in large trees with mean 101.1 ± 28.6 cm dbh (range 50–184 cm), in cavities located 18 ± 5.1 m above the ground (range 8.1–29.5 m), with a wide 23.5 ± 12.7 cm entrance diameter (range 8–73 cm), and large 45.5 ± 17.6 cm internal diameter (range 14–81 cm), that were on average about a meter deep (mean 93 ± 65.1 cm; range 5–280 cm; Table 1).

Insert Figure 1

Insert Table 1

Tree-cavity availability

We recorded a total of 57 cavities in 24 ha of tropical moist forest, however two cavities had entrance diameters <7 cm, and therefore were not available for use by parrots. Of the 55 available cavities, 30 were located in primary evergreen forest, 15 in primary riparian forest, and 10 in secondary forest. The majority of available cavities were formed by decay (85.5%; n = 47) and occurred in live trees (78.2%; n = 43), with most cavities located on the main trunk (77.8%; n = 35).

There was an overall density of 2.3 cavities/ha available for use by Northern Mealy Amazons in tropical moist forest, but number of available cavities per survey plot differed significantly among vegetation types (Table 2). In particular, survey plots in primary evergreen forest had significantly more cavities than survey plots in secondary forest (q =2.8, $P < 0.01$). Furthermore, cavities in secondary forest occurred in significantly smaller trees compared to cavities in primary evergreen (tree dbh: $q = 3.5$, $P < 0.05$) and riparian forest (tree dbh: $q = 4.5$, $P < 0.01$; support diameter: $q = 2.6$, $P < 0.01$; Table 2). Cavities in secondary forest also had smaller entrance dimensions than cavities in primary riparian forest (entrance length: $q = 2.4$, $P < 0.02$; Table 2).

Insert Table 2

Only 38 cavities had characteristics within the range of those used as nest-sites by Northern Mealy Amazons (height above the ground ≥8.1 m, entrance diameter ≥8 cm, internal diameter ≥14 cm, and depth ≥5 cm), giving an overall density of 1.6 cavities/ha with characteristics suitable for nesting by Northern Mealy Amazons. These suitable cavities were concentrated in primary evergreen (2.1 suitable cavities/ha) and riparian forest (1.9 suitable cavities/ha), with only 0.75 suitable cavities/ha in secondary forest.

Nest-site selection by Northern Mealy Amazons

Overall, the use of tree species as nest-sites by Northern Mealy Amazons did not differ significantly from that expected by the availability of accessible cavities in those tree species ($G_{12} = 15.5$, $P = 0.23$). Only in the case of *Ficus* sp. and *Poulsenia armata*, Northern Mealy Amazons used these tree species as nest-sites less than may be expected by their cavity availability (Figure 1). However, in both cases the expected proportion only marginally fell outside the confidence intervals (CI) for the observed proportion of use (*Ficus* sp.: Expected = 0.18, Observed CI = 0–0.15; *P. armata*: Expected = 0.12, Observed CI = 0–0.10).

On the other hand, use and availability comparisons determined that Northern Mealy Amazons selected nest-sites based on cavity characteristics. Univariate analyses found significant differences in each cavity characteristic variable between cavities used as nests by Northern Mealy Amazons and available cavities (Table 1). Cavities used as nests by Northern Mealy Amazons occurred in significantly larger trees, at a greater height above the ground, and with larger internal diameter, and greater depth than most of the cavities available for parrots (Table 1). These variables were significantly different even after Bonferroni alpha adjustment to $P < 0.007$.

The multiple logistic regression model determined that cavity characteristics explained nest-site use by parrots, where cavity depth (Wald $X^2_1 = 3.9$, $P = 0.047$), and internal diameter (Wald $X^2_1 = 5.2$, $P = 0.022$) significantly predicted selection of a cavity as a nest-site by the Northern Mealy Amazon. The odds that a cavity would be selected as a nest were raised by 1.4 for each increase in internal diameter, and 1.1 for each increase in cavity depth. Calculation of the inflection point for the probability curve demonstrated that a cavity had a greater than 50% chance of being selected as a nest-site if this had >29.5 cm internal diameter, and was >45.9 cm deep.

Discussion

Nest-site requirements of the Northern Mealy Amazon

The Northern Mealy Amazon nested in a variety of tree species in Los Chimalapas, Mexico, but demonstrated a narrow niche-breadth of nesting tree species, using predominantly nest-cavities in live trees of *Terminalia amazonia* and *Dialium guianense*. This is similar to the variety of 22 tree species used as nest-sites by the Northern Mealy Amazon in the Petén of Guatemala, where *T. amazonia* was also the tree species most frequently used for nesting (Bjork, 2004). Other species of Psittaciformes also use predominantly 1-3 tree species for nesting (Cameron, 2006; de la Parra-Martínez, Renton, Salinas-Melgoza, & Muñoz-Lacy, 2015; Monterrubio-Rico, Ortega-Rodríguez, Marín-Togo, Salinas-Melgoza, & Renton, 2009; Renton & Brightsmith, 2009; Renton, Salinas-Melgoza, De Labra-Hernández, & de la Parra-Martínez, 2015; Robinet & Salas, 1999; Symes & Perrin, 2004). However, although Northern Mealy Amazons nested most frequently in cavities in *T. amazonia* and *D. guianense*, they used these tree species for nesting according to their availability of cavities for parrots. This is similar to the Yellow-crowned Amazon (*Amazona* *ochrocephala*) in Panama, which uses tree species for nesting according to the availability of cavities in those trees (Rodríguez & Eberhard, 2006), but contrasts with the large Military Macaw (*Ara militaris*), which selects large emergent tree species for nesting (de la Parra-Martínez, Renton, Salinas-Melgoza, & Muñoz-Lacy, 2015).

Nevertheless, Northern Mealy Amazons used cavities in *Ficus* sp. and *Poulsenia armata* slightly less than may be expected by the availability of cavities in these trees. Similarly, the Northern Mealy Amazon in Guatemala rarely used these tree species as nest-sites (Bjork 2004). Both these species are softwood trees in the Moraceae family of latex producing plants (Pennington & Sarukhan, 1998), and may have structural properties that make them less desirable as a nest-site. The Blue-fronted Parrot (*Amazona aestiva*) was more likely to reuse deep cavities with thick walls (Berkunsky & Reboreda, 2009), and cavities in large, living trees with thick walls tend to maintain more stable temperatures (Maziarz & Wesolowski, 2013; Wiebe, 2001), although microclimatic condition of cavities does not have a large effect on reproductive output (Wiebe, 2001). Nevertheless, we did not evaluate the internal condition of available cavities, therefore there may be other microclimatic factors making cavities less suitable for use as a nest-site by the Northern Mealy Amazon.

We found that the Northern Mealy Amazon used nest-cavities in large trees of mean 1 m dbh, at a mean 18 m height above the ground, with large mean 23.5 cm entrance diameter, and mean 45.5 cm internal diameter, that were of mean 93 cm deep. Characteristics of nest-sites did not vary among primary and secondary forest or in pastures at the forest edge, as Northern Mealy Amazon nests generally occurred in remnant canopy trees characteristic of primary forest. Most Amazon parrots use nest-cavities at a lower mean height, and of smaller mean entrance and internal diameters (Berkunsky & Reboreda, 2009; Enkerlin-Hoeflich, 1995; Renton & Salinas-Melgoza, 1999; Rivera, Politi, & Bucher, 2012; Rodríguez & Eberhard, 2006; Snyder, Wiley, & Kepler, 1987) than that found for the Northern Mealy Amazon in our study. In fact, the mean nest-site characteristics of tree dbh, height above the ground, entrance diameter, and internal diameter place the Northern Mealy Amazon among the upper quartile of species of Psittaciformes that require large nest-cavities, located high above the ground in large, mature canopy trees (Renton, Salinas-Melgoza, De Labra-Hernández, & de la Parra-Martínez, 2015). In particular, the large entrance and internal diameters of Northern Mealy Amazon nests were more similar to those used by large macaws and cockatoos (Berkunsky et al., 2014; Heinsohn, Murphy, & Legge, 2003; Olah, Vigo, Heinsohn, & Brightsmith, 2014; Saunders, Mawson, & Dawson, 2014). Indeed, only about 10% of studied Psittaciformes used nest-cavities with larger mean entrance and internal diameters (Renton, Salinas-Melgoza, De Labra-Hernández, & de la Parra-Martínez, 2015). The Northern Mealy Amazon may need to use large nest-cavities to contain the brood. However, the use of nest-cavities with large entrance diameters may permit access by a greater variety of predators, increasing the risks of nest predation for the Northern Mealy Amazon.

Nest-site selection by the Northern Mealy Amazon

As found for other parrot species (Renton, Salinas-Melgoza, De Labra-Hernández, & de la Parra-Martínez, 2015), the Northern Mealy Amazon selected nest-sites based on cavity dimensions. Parrots selected as nest-sites cavities in larger trees, at a greater height above the ground, and with larger entrance and internal diameters, and greater depth, from the resource of cavities available to them in the landscape. Height of the cavity entrance from the ground is an important criterion for nest-site selection for many cavity-nesting birds (Cockle, Martin, & Wiebe, 2011; Li & Martin, 1991; Nilsson, 1984), and is a key factor influencing predation rate of nests (Li & Martin, 1991; Nilsson, 1984; Wilcove, 1985). Furthermore, cavity height above the ground is a significant predictor of nest success for some parrot species (Berkunsky & Reboreda, 2009, Cockle, Bodrati, Lammertink, & Martin, 2015). Hence, the selection of nest-cavities high above the ground by the Northern Mealy Amazon may be a strategy to reduce predation risk and increase the probability of nest success.

In particular, cavity depth and internal diameter predicted selection of a cavity as a nest-site by the Northern Mealy Amazon. Cavity depth was found to influence nest success of the Eclectus Parrot (*Eclectus roratus*), with deeper nests producing a greater number of fledglings (Heinsohn, 2008). The importance of internal diameter of the cavity as a criterion predicting nest-site selection may reflect the requirement for a large nest chamber able to accommodate the nest contents for this large-bodied parrot. The Northern Mealy Amazon is the largest Amazon parrot in continental America, only exceeded in size by two Caribbean island parrot species (Forshaw, 1989). Internal diameter of the nest-cavity was found to significantly influence hatching success of the Scarlet Macaw (*Ara macao*) in Peru, with eggs more likely to hatch in nests with larger internal diameters (Olah, Vigo, Heinsohn, & Brightsmith, 2014). Therefore, the selection of deep cavities with larger internal diameters may increase the probability of nest-success and reproductive output for large-bodied parrots such as the Northern Mealy Amazon.

Cavity availability for Northern Mealy Amazons

As found for other tropical forests (Cockle, Martin, & Wesolowski, 2011; Vázquez & Renton, 2015), the majority of tree-cavities in the tropical moist forest of Los Chimalapas were formed by decay processes. We found a low overall density of 2.4 cavities/ha in the tropical moist forest of Los Chimalapas, with 2.3 cavities/ha available for Northern Mealy Amazons. Even considering just conserved evergreen and riparian forest, there were only 2.9 cavities/ha (2.8 available cavities/ha). This is much lower than cavity densities recorded in other tropical moist forests of continental America, ranging from 16.8-111.7 cavities/ha (Boyle, Ganong, Clark, & Hast, 2008; Saunders, Smith, & Rowley, 1982), with a density of 4.5 cavities/ha suitable for nesting by birds (Cockle, Martin, & Drever, 2010).

Furthermore, in Los Chimalapas only 1.6 cavities/ha had characteristics suitable for nesting by Northern Mealy Amazons. Studies of smaller-bodied Amazon parrot species have found higher densities of 4.6–11.3 suitable cavities/ha (Rivera, Politi, & Bucher, 2012; Snyder, Wiley, & Kepler, 1987). Only in the case of large-bodied macaws or cockatoos have lower densities of 0.3–0.7 suitable cavities/ha been recorded (de la Parra-Martínez, Renton, Salinas-Melgoza, & Muñoz-Lacy, 2015; Marsden & Pilgrim, 2003; Walker, Cahill, & Marsden, 2005). This low density of tree-cavities suitable for nesting by the Northern Mealy Amazon may be a limiting factor on the number of nesting pairs, creating competition for nest-sites (Heinsohn, Murphy, & Legge, 2003; Newton, 1994). During the present study, we observed agonistic interactions among four pairs of Northern Mealy Amazons for occupancy of a suitable nest-cavity. Interspecific competition may also limit the availability of nest-cavities for the Northern Mealy Amazon as during the parrot nesting seasons of 2014-2016, we found potential nest-cavities occupied by other secondary cavity-nesters, including the Guatemalan Screech Owl (*Megascops guatemalae*), Bat Falcon (*Falco rufigularis*), Keel-billed Toucan (*Ramphastos sulfuratus*), and Kinkajou (*Potus flavus*).

We found the lowest density of 1.3 available cavities/ha in secondary forest, where only 0.75 cavities/ha were suitable for nesting by Northern Mealy Amazons. Other studies have also found a generally low density of 0.5–1.64 cavities/ha suitable for birds in disturbed or human-managed forests (Cockle, Martin, & Drever, 2010; Cockle, Martin, & Wiebe, 2008; Politi, Hunter, & Rivera, 2010). As determined in the present study, available tree-cavities in secondary forest occurred in smaller trees, and had smaller dimensions than in primary forest. Therefore, the increasing transformation of primary tropical moist forest to secondary forest (de Jong et al., 2010) is likely to have consequences in reducing the availability of suitable nest-sites for large-bodied secondary cavity-nesters. Furthermore, as highlighted by Marsden and Pilgrim (2003), long-lived parrots may be able to utilize food resources in disturbed or managed forests, but the reduction in density of suitable nest-sites in modified forests puts at risk the persistence of wild populations in the long-term.

Implications for Conservation

Our study demonstrated a low density of suitable nest-sites for the Northern Mealy Amazon, which were concentrated in primary tropical moist forest. Secondary forest provided few nest-site resources for this large-bodied threatened parrot species. Furthermore, the Northern Mealy Amazon was highly selective in use of nest-sites, with suitable nest-cavities having characteristics indicative of large, old primary forest trees. Given these specific nest-site requirements of the Northern Mealy Amazon, long-term persistence of the species in Mesoamerica depends in part on maintaining the availability of suitable nest-sites through appropriate forestry practices.

The Northern Mealy Amazon depends on the maintenance of large, mature trees that can provide the large cavity dimensions required for nest-sites, most of which occur in emergent tree species of *Terminalia amazonia* and *Dialium guianense*. However, these hardwood tree species are frequently cut for use in heavy construction (Pennington & Sarukhán, 1998). Incentives should be provided to maintain large trees (>1m dbh) in agricultural landscapes as these are more susceptible to selective logging (Gibbons et al., 2008). Compensation or gratification schemes paid to local landowners who protect

Northern Mealy Amazon nests on their land could also be implemented to promote the protection of active parrot nests.

Existing legislation may be employed to limit deforestation along watercourses. The 1992 National Water Law in Mexico establishes 10 m either side of watercourses as federal land, while the NOM-152-SEMARNAT-2006 regulation specifies that forestry management programs should maintain riparian vegetation 20 m either side of permanent rivers. This could provide the basis for local land-use strategies to maintain riparian forest within a 20-50 m band along permanent rivers thereby preserving some large, cavity-bearing trees. Riparian forests have an added contribution as corridors connecting forest patches in modified landscapes and maintaining animal movements (Gillies & St. Clair, 2008; Lees & Peres, 2008). However, given that our study determined the greatest density of available cavities in tropical moist evergreen forest, and that the most frequently used nest-tree species were characteristic of evergreen forest (Rzedowski, 2006; Torres Colín, 2004), it would still be important to implement strategies to conserve primary evergreen forest to provide adequate nest-sites for large-bodied, threatened secondary cavity-nesters.

Strategies such as conservation set-aside schemes could be implemented in Los Chimalapas and focused on conserving extensive areas of primary evergreen forest. Old growth forests provide a greater number of hollow-bearing trees, with older trees able to form larger cavities (Lindenmayer, Cunningham, Nix, Tanton, & Smith, 1991). Large mature trees are a key resource in forest ecosystems but are rapidly being lost worldwide (Gibbons et al., 2008; Lindenmayer, Laurance, & Franklin, 2012). Therefore, the implementation of a suite of strategies to promote the maintenance of large, mature trees would not only be of benefit for reproduction of the Northern Mealy Amazon, but would also contribute to maintaining biodiversity and ecosystem integrity.

Acknowledgements

The study was conducted in partial fulfillment of a Ph.D. degree by MADLH at the Posgrado en Ciencias Biologicas, of the Universidad Nacional Autónoma de México (UNAM). Funding for the research was provided by the Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (UNAM-DGAPA-PAPIIT grant IN205716) to KR. MADLH received a Doctoral studies grant from the Consejo Nacional de Ciencia y Tecnología (Conacyt 215549). We are grateful to Idea Wild who provided field equipment, and to Alvaro Campos who assisted with taxonomic identification of tree species. The Secretaria del Medio Ambiente y Recursos Naturales in Mexico provided research permits for the study. We are grateful to the authorities of the Santa María Chimalapa municipality for permission to work on their community lands, and to the local people of San Francisco La Paz, La Fortaleza, San Antonio Nuevo Paraíso and Chalchijapa who provided assistance in the field.

Declaration of Conflicting Interests

The authors declared no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Funding

Funding for the research was provided by the Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (UNAM-DGAPA-PAPIIT grant IN205716) to KR. MADLH received a Doctoral studies grant from the Consejo Nacional de Ciencia y Tecnología (Conacyt 215549).

References

Aitken, K. E. H., & Martin, K. (2007). The importance of excavator in hole-nesting communities: Availability and use of natural tree-holes in old mixed-forest of western Canada. *Journal of Ornithology*, *148*, S425–S434.

Berkunsky, I., Daniele, G., Kacoliris, F. P., Diaz-Luque, J. A., Silva Frias, C. P., Aramburu, R. M., & Gilardi, J. D. (2014). Reproductive parameters in the critically endangered Blue-throated Macaw: Limits to the recovery of a parrot under intensive management. *Plos ONE*, doi:10.1371/journal.pone.0099941.

Berkunsky, I., & Reboreda, J. C. (2009). Nest-site fidelity and cavity reoccupation by Blue-fronted Parrots *Amazona aestiva* in the dry Chaco of Argentina. *Ibis*, *151*, 145–150.

BirdLife International [BI] (2016). *Species factsheet*: *Amazona guatemalae*. Retrieved from http://www.birdlife.org/datazone/species/factsheet/45430583

Bjork, R. (2004). *Delineating patterns and process in tropical lowlands: Mealy Parrot migration dynamics as a guide for regional conservation planning* (Ph.D. thesis), Oregon State University, Oregon, USA. Retrieved from http://ir.library.oregonstate.edu/xmlui/handle/1957/10842

Brightsmith, D., & Bravo, A. (2006). Ecology and management of nesting blue-and-yellow macaws (*Ara ararauna*) in Mauritia palm swamps. *Biodiversity and Conservation*, *15*, 4271–4287

Boyle, W. A., Ganong, C. N., Clark, D. B., & Hast, M. A. (2008). Density, distribution, and attributes of tree cavities in old-growth tropical rain forest. *Biotropica*, *40*, 241–245.

Byers, C. R., Steinhorst, R. K., & Krausman, P. R. (1984). Clarification of a technique for analysis of utilization-availability data. *Journal of Wildlife Management*, *48*, 1050–1053.

Cameron, M. (2006). Nesting habitat of the Glossy Black-Cockatoo in central New South Wales. *Biological Conservation*, *127*, 402–410.

Cockle, K., Bodrati, A., Lammertink, M., & Martin, K. (2015). Cavity characteristics, but not habitat, influence nest survival of cavity-nesting birds along a gradient of human impact in the subtropical Atlantic Forest. *Biological Conservation*, *184*, 193–200.

Cockle, K. L., Martin, K., & Drever, M. C. (2010). Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. *Biological Conservation*, *143*, 2851–2857.

Cockle, K. L., Martin, K., & Wesolowski, T. (2011). Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. *Frontiers in Ecology and Environment*, *9*, 377–382.

Cockle, K., Martin, K., & Wiebe, K. (2008). Availability of cavities for nesting birds in the Atlantic forest, Argentina. *Ornitologia Neotropical*, *19*, 269–278.

Cockle, K., Martin, K., & Wiebe, K. (2011). Selection of nest trees by cavity-nesting birds in the Neotropical Atlantic forest. *Biotropica*, *43*, 228–236.

Colwell, R. K., & Futuyma, D. J. (1971). On the measurement of niche breadth and overlap. *Ecology*, *52*, 567–576.

de Jong, B., Anaya, C., Masera, O., Olguin, M., Paz, F., Etchevers, J.,. . . Balbontin, C. (2010). Greenhouse gas emissions between 1993 and 2002 from land-use change and forestry in Mexico. *Forest Ecology and Management*, *260*, 1689–1701.

de la Parra-Martínez, S. M., Renton, K., Salinas-Melgoza, A., & Muñoz-Lacy, L. G. (2015). Tree-cavity availability and selection by a large-bodied secondary cavity-nester: The Military Macaw. *Journal of Ornithology*, *156*, 489–498. doi 10.1007/s10336-014-1150-9.

Enkerlin-Hoeflich, E. C. (1995). *Comparative ecology and reproductive biology of three species of Amazona parrots in norhteastem Mexico* (Ph.D. Thesis), Texas A&M University, Texas, USA.

Forshaw, J. M. 1989. *Parrots of the world.* Third Edition. Melbourne, Australia: Lansdowne Editions.

Gibbons, P., Lindenmayer, D. B., Fischer, J., Manning, A. D., Weinberg, A., Seddon, J.,. . . Barrett, G. (2008). The future of scattered trees in agricultural landscapes. *Conservation Biology, 22*, 1309–1319.

Gillies, C., & St. Clair, C. C. (2008). Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. *Proceedings of the National Academy of Science USA, 105*, 19774–17779.

Heinsohn, R. (2008). The ecological basis of unusual sex roles in reverse-dichromatic Eclectus parrots. *Animal Behaviour*, *76*, 97–103.

Heinsohn, R., Murphy, S., & Legge, S. (2003). Overlap and competition for nest holes among Eclectus Parrots, Palm Cockatoos and Sulphur-crested Cockatoos. *Australian Journal of Zoology*, *51*, 81–94.

Houle, A., Chapman, C. A., & Vickery, W. L. (2004). Tree climbing strategies for primate ecological studies. *International Journal of Primatology*, *25*, 237–260.

Lees, A. C., & Peres, C. A. (2008). Conservation value of remnant riparian forest corridors of varying quality for Amazonian birds and mammals*. Conservation Biology, 22*, 439–449.

Levins, R. (1968). *Evolution in changing environments*. Princeton, N.J.: Princeton University Press.

Li, P., & Martin, T. E. (1991). Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. *Auk*, *108*, 405–418.

Lindenmayer, D. B., Cunningham, R. B., Nix, H. A., Tanton, M. T., & Smith, A. P. (1991). Predicting the abundance of hollow-bearing trees in montane forests of southeastern Australia. *Australian Journal of Ecology*, *16*, 91–98.

Lindenmayer, D. B., Laurance, W. F., & Franklin, J. F. (2012). Global decline in large old trees. *Science*, *338*, 1305–1306.

Marsden, S. J., & Pilgrim, J. D. (2003). Factors influencing the abundance of parrots and hornbill in pristine and disturbed forests on New Britain. *Ibis*, *145*, 45–53.

Martínez-Pacheco, A. I. (2012). Monitoreo del cambio de uso de suelo en Los Chimalapas 2000-2003 [Monitoring land-use change in Los Chimalapas 2000-2003]. In D. Ortega del Valle, T., Carranza López, & J. Martínez Pérez (Eds.). *Una mirada desde el corazón de la jícara de oro. Experiencias de conservación en la Selva Zoque de Los Chimalapas* [*A look from the heart of the golden gourd. Conservation experiences in the Zoque forest of Los Chimalapas*] (pp. 86–94). Oaxaca, Mexico: WWF-Mexico.

Maziarz, M., & Wesolowski, T. (2013). Microclimate of tree cavities used by Great Tits (*Parus major*) in a primeval forest. *Avian Biology Research, 6,* 47–56.

Monterrubio-Rico, T. C., & Escalante-Pliego, P. (2006). Richness, distribution and conservation of cavity nesting birds in Mexico. *Biological Conservation*, *128*, 67–78.

Monterrubio-Rico T. C., Ortega-Rodríguez, J., Marín-Togo, M. C., Salinas-Melgoza, A., & Renton, K. (2009). Nesting habitat of the Lilac-crowned Parrot in a modified landscape in Mexico. *Biotropica*, *41*, 361–368.

Newton, I. (1994). The role of nest sites in limiting the numbers of hole-nesting birds: A review. *Biological Conservation*, *70*, 265–76.

Nilsson, S. G. (1984). The evolution of nest-site selection among hole-nesting birds: The importance of nest predation and competition. *Ornis Scandinsvica*, *15*, 167–175.

Nue, A. W., Byers, C. R., & Peek, J. M. (1974). A technique for analysis of utilization-availability data. *Journal of Wildlife Management*, *38*, 541–545.

Olah, G., Butchart, S. H. M., Symes, A., Medina Guzmán, I., Cunningham, R., Brightsmith, D. J., & Heinsohn, R. (2016). Ecological and socio-economic factors affecting extinction risk in parrots. *Biodiversity and Conservation, 25,* 205–223

Olah, G., Vigo, G., Heinsohn, R., & Brightsmith, D. J. (2014). Nest site selection and efficacy of artificial nests for breeding success of Scarlet Macaw *Ara macao* in lowland Peru. *Journal for Nature Conservation*, *22*, 176–185.

Pennington, T. D., & Sarukhán, J. (1998). *Árboles tropicales de México* [*Tropical trees of Mexico*]. Second Edition. Mexico City: Fondo de Cultura Económica.

Perry, D. R., & Williams, J. (1981). The tropical rain forest canopy: A method providing total access. *Biotropica*, *13*, 283–285.

Politi, N., Hunter, M., Jr., & Rivera, L. (2009). Nest selection by cavity nesting birds in subtropical montane forests of the Andes. *Biotropica*, *4*, 354–360.

Politi, N., Hunter, M., Jr., & Rivera, L. (2010). Availability of cavities for avian cavity nester in selectively logged subtropical montane forest of the Andes. *Forest Ecology and Management*, *260*, 893–906.

Quinn, G. P., & Keough, M. J. (2002). *Experimental design and data analysis for biologists*. Cambridge: Cambridge University Press.

Renton, K., & Brightsmith, D. J. (2009). Cavity use and reproductive success of nesting macaws in lowland forest of southeast Peru. *Journal of Field Ornithology, 80*, 1–8.

Renton, K., & Salinas-Melgoza, A. (1999). Nesting behavior of the Lilac-crowned Parrot. *Wilson Bulletin*, *111*, 488–493.

Renton, K., Salinas-Melgoza, A., De Labra-Hernández, M. A., & de la Parra-Martínez, S. M. (2015). Resource requirements of parrots: Nest site selectivity and dietary plasticity of Psittaciformes. *Journal of Ornithology*, *156*, S73-S90. doi: 10.1007/s10336-015-1255-9.

Rivera, L., Politi, N., & Bucher, E. H. (2012). Nesting habitat of the Tucuman Parrot *Amazona tucumana* in an old growth cloud forest of Argentina. *Bird Conservation International*, *22*, 398–410.

Robinet, O., & Salas, M. (1999). Reproductive biology of the endangered Ouvea Parakeet *Eunymphicus cornutus uvaeensis*. *Ibis*, *141*, 660–669.

Rodríguez, A. M., & Eberhard, J. R. (2006). Reproductive behavior of the Yellow-crowned Parrot (*Amazona ochrocephala*) in western Panama. *Wilson Journal of Ornithology*, *118*, 255–236.

Rzedowski, J. (2006). *Vegetación de México* [*Vegetation of Mexico*]. First Digital Edition. Mexico City: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad. Retrieved from http://www.biodiversidad.gob.mx/publicaciones/librosDig/pdf/VegetacionMx_Cont.pdf

Saunders, D. A., Mawson, P. R., & Dawson, R. (2014). Use of tree hollows by Carnaby's Cockatoo and the fate of large hollow-bearing trees at Coomallo Creek, Western Australia 1969–2013. *Biological Conservation*, *177*, 85–193.

Saunders, D. A., Smith, G. T., & Rowley, I. (1982). The availability and dimensions of tree hollows that provide nest sites for cockatoos (Psittaciformes) in Western Australia. *Australian Wildlife Research*, *9*, 541–556.

Snyder, N. F. R., Wiley J. W., & Kepler, C. B. (1987). *The parrots of Luquillo: Natural history and conservation of the Puerto Rican Parrot*. Los Angeles, California: Western Foundation of Vertebrate Zoology.

Stojanovic, D, Webb, M., Roshier, D., Saunders, D., & Heinsohn, R. (2012). Ground-based survey methods both overestimate and underestimate the abundance of suitable tree-cavities for the endangered Swift Parrot. *Emu*, *112*, 350–356.

Symes, T. A., & Perrin, M. R. (2004). Breeding biology of the Greyheaded Parrot (*Poicephalus fuscicollis*) in the wild. *Emu*, *104*, 45–57.

Torres Colín, R. (2004). Tipos de vegetación [Vegetation types]. In A. J. García-Mendoza, M. J., Ordoñez, & M. Briones-Salas (Eds.). *Biodiversidad de Oaxaca* [*Biodiversity of Oaxaca*] (pp. 105–117). Mexico City: Instituto de Biología, UNAM, Fondo Oaxaqueño para la Conservación de la Naturaleza, WWF-Mexico.

Trejo, I. (2004). Clima [Climate]. In A. J. García-Mendoza, M. J., Ordoñez, & M. Briones-Salas (Eds.). *Biodiversidad de Oaxaca* [*Biodiversity of Oaxaca*] (pp. 67–85). Mexico City: Instituto de Biología, UNAM, Fondo Oaxaqueño para la Conservación de la Naturaleza, WWF-Mexico.

Vázquez, L. D., & Renton, K. (2015). High density of tree-cavities and snags in tropical dry forest of western Mexico raises questions for a latitudinal gradient. *PLoS ONE*, 10, e0116745. doi:10.1371/journal.pone.0116745.

Walker, J. S., Cahill, A. J., & Marsden, S. J. (2005). Factors influencing nest-site occupancy and low reproductive output in the critically endangered Yellow-crested Cockatoo *Cacatua sulphurea* on Sumba, Indonesia. *Bird Conservation International*, *15*, 347–359.

Wenner, T. J. Russello, M. A., & Wright, T. F. (2012). Cryptic species in a Neotropical parrot: genetic variation within the *Amazona farinosa* species complex and its conservation implications. *Conservation Genetics*, *13*, 1427–1432.

Wiebe, K. L. (2001). Microclimate of tree cavity nests: Is it important for reproductive success in Northern Flickers? *Auk, 118*, 412–421.

Wilcove, D. S. (1985). Nest predation in forest tracts and the decline of migratory songbirds. *Ecology*, *66*, 1211–1214.

Zar, J. H. (1999). *Biostatistical analysis*. Fourth Edition. New Jersey, USA: Prentice Hall Inc.

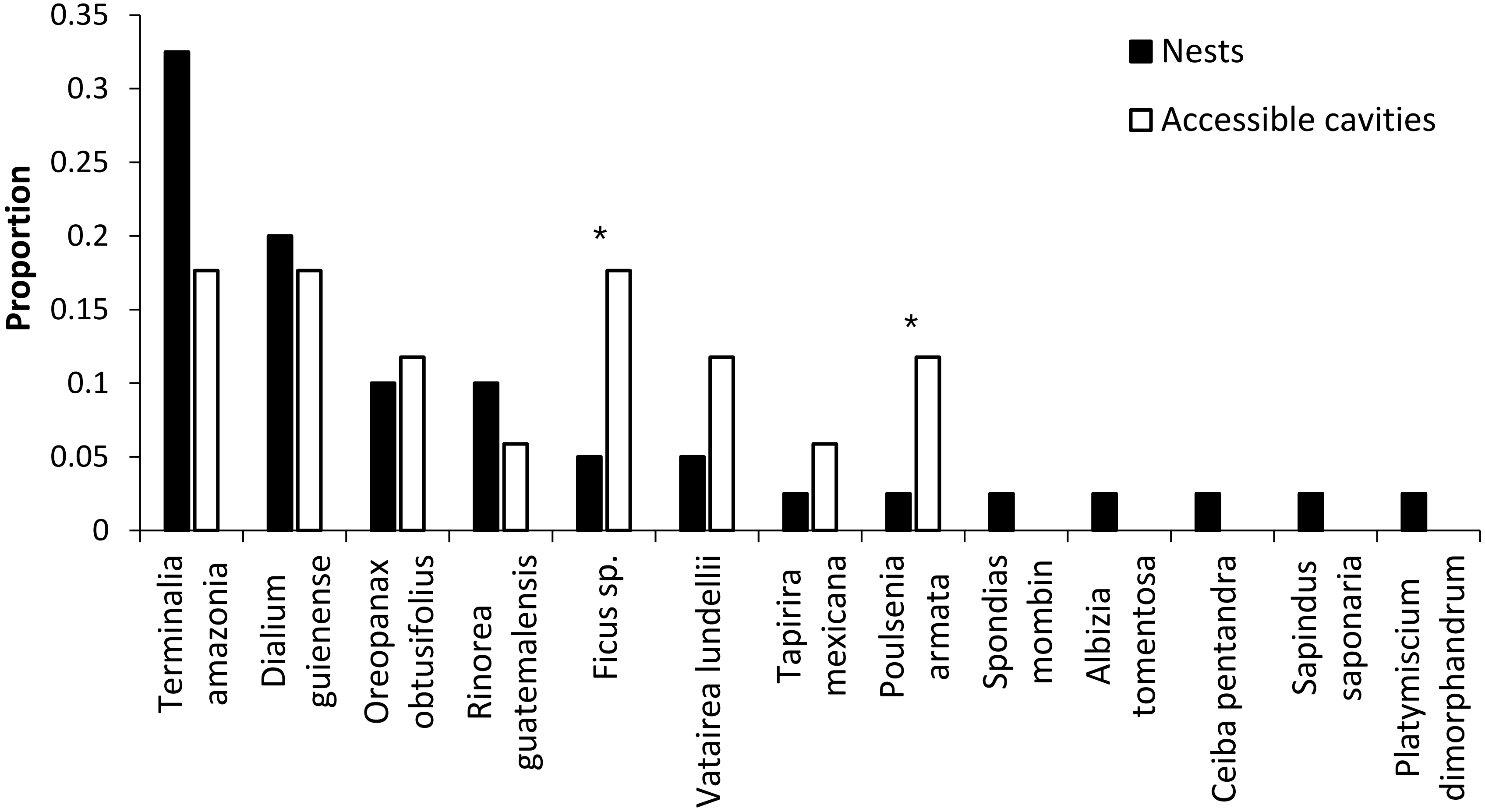
Table 1. Characteristics (mean ± SD) of tree-cavities used as nests by the Northern Mealy Amazon (*Amazona guatemalae*) and all accessible cavities (≥7.0 cm entrance diameter) in tropical moist forest of Los Chimalapas, Mexico, with Mann-Whitney U test of significance

Variable	Nest cavities (N = 40)	Accessible cavities (N = 55)	Significance values
Tree diameter at breast height (cm)	101.1 ± 28.6	64.9 ± 29.3	$U_{40,52} = 415.5$, $P < 0.001$*
Cavity height above the ground (m)	18.0 ± 5.1	12.4 ± 5.0	$U_{40,55} = 458.0$, $P < 0.001$*
Entrance width (cm)	23.5 ± 12.7	17.4 ± 6.9	$U_{39,51} = 689.0$, $P = 0.013$
Entrance length (cm)	42.1 ± 20.2	29.8 ± 17.9	$U_{35,51} = 545.5$, $P = 0.001$*
Cavity depth (cm)	93 ± 65.1	22.7 ± 14.9	$U_{40,45} = 278.0$, $P < 0.001$*
Internal diameter (cm)	45.5 ± 17.6	19.3 ± 8.1	$U_{40,45} = 137.0$, $P < 0.001$*
Support diameter (cm)	70.6 ± 26.6	38.2 ± 17.5	$U_{40,51} = 285.5$, $P < 0.001$*

Table 2. Mean (± SD) characteristics of cavities available for the Northern Mealy Amazon (≥7 cm entrance diameter) in three forest types at Los Chimalapas, Mexico, with parametric (one-way ANOVA) and nonparametric (Kruskal-Wallis ANOVA) test of significance. Letters indicate significantly different posthoc pairwise comparisons among forest types.

Variables	Evergreen (N = 30)	Riparian (N = 15)	Secondary (N = 10)	Significance values
Cavities/1-ha survey plot	3.3 ± 1.1^{a}	2.1 ± 1.8^{ab}	1.3 ± 1.0^{b}	$H_{2,24}$ = 8.2, P=0.016
Tree diameter at breast height (cm)	66.3 ± 30.2^{a}	76.8 ± 26.4^{a}	40.6 ± 15.3^{b}	$F_{2,49}$ = 5.1, P = 0.01
Cavity height above the ground (m)	12.3 ± 6.0	14.2 ± 3.1	10.4 ± 3.3	$F_{2,52}$ = 1.8, P = 0.18
Entrance length (cm)	29.7 ± 14.7 ^{ab}	38.5 ± 26.6 ^{a}	20.4 ± 10.7 ^{b}	$H_{2,51}$ = 6.0, P = 0.049
Entrance width (cm)	17.5 ± 5.3	19.6 ± 10.7	14.6 ± 6.1	$F_{2,48}$ = 1.4, P = 0.26
Cavity depth (cm)	22.5 ± 15.3	29.4 ± 17.2	15.8 ± 6.6	$H_{2,45}$ = 3.6, P = 0.17
Internal diameter (cm)	17.5 ± 5.6	23.3 ± 12.7	19.3 ± 5.5	$F_{2,42}$ = 2.0, P = 0.15
Support diameter (cm)	37.6 ± 16.3^{ab}	49.2 ± 21.4^{a}	27.8 ± 8.2^{b}	$H_{2,51}$ = 6.7, P = 0.035

Figure 1. Proportion of tree species used as nests by the Northern Mealy Amazon (*Amazona guatemalae*), and available cavities (entrance ≥7 cm) in each tree species in the tropical moist forest of Los Chimalapas, Oaxaca. * = expected proportion based on availability falls outside the confidence intervals for observed use of each tree species.



CAPÍTULO III

(Preparado para *Journal of Field Ornithology*)

Differential value of forest types for foraging Northern Mealy Amazons in a modified landscape of tropical moist forest

Miguel A. De Labra-Hernández,[1] and Katherine Renton[2,3]

[1] *Posgrado en Ciencias Biológicas, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico*.

[2] *Estación de Biología Chamela, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 21, San Patricio-Melaque, Jalisco, Mexico*.

[3] Corresponding Author. Email: krenton@ib.unam.mx

Abstract

The Northern Mealy Amazon (*Amazona guatemalae*) is one of the largest amazon species in continental America, and inhabits tropical moist forest that is undergoing high rates of fragmentation and conversion to secondary forest. Little is known of the food resource requirements of the Northern Mealy Amazon, or whether parrots may be affected by variations in food resource availability in modified landscapes. We determined the diet of the Northern Mealy Amazon through observations of foraging parrots in Los Chimalapas, Mexico. We also established 30 phenology transects (200 x 6 m) to determine food resource availability in three vegetation types of primary tropical moist and riparian forest, as well as secondary forest during the parrot breeding (March-April) and non-breeding (August-September) season. We found spatial-temporal variation in food resource availability, with significantly greater availability of food resources in the breeding season compared to the non-breeding season, and significantly fewer resources in secondary forest. Parrots consumed mainly seeds of a variety of plant species, and presented a broad dietary niche during the breeding season. Parrots did not select resource items in the diet, but rather consumed items according to their availability. This generalist foraging strategy may enable parrots to rapidly adapt to spatial-temporal variations in food resource availability. Primary tropical moist forest may be a key habitat type for Northern Mealy Parrots during the breeding season as this provides an abundance of food resources for parrots when they are raising young.

Key words: *Amazona guatemalae*, fruit availability, fruit-tracking, habitat degradation, Los Chimalapas, Mesoamerica, Psittaciformes

Resource selection occurs through the disproportionate use of resources compared to their availability (Johnson 1980, Jones 2001). However, resources are not distributed uniformly in the environment, but may exhibit high heterogeneity among patches (MacArthur and Pianka 1966). Such differential or unpredictable variability in abundance of food resources should favor the development of generalist feeding strategies (Schoener 1971). Hence, under conditions of environmental uncertainty animals should exhibit broad niches (MacArthur and Levins 1967), and undertake frequent sampling of resource patches to evaluate availability (Clark and Mangel 1984). These strategies employ a learning by consequence foraging model that enables individuals to rapidly adapt to environmental changes (Provenza and Cincotta 1993).

Psittaciformes (parrots) consume fruits and seeds of a variety of plant species (Renton et al. 2015), that even in the tropics may exhibit high temporal and spatial variations in abundance (Bullock and Solís-Magallanes 1990, White 1994, Morellato et al. 2013). However, few studies have evaluated food resource selection by parrots (Renton et al. 2015); although Robinet et al. (2003) found that the Ouvea Parakeet (*Eunymphicus uvaeensis*) selects plant species that produce fruit throughout the year. Other studies have determined that parrots adjust dietary niche breadth with fluctuations in food resource availability (Renton 2001; Diaz et al. 2012), suggesting that they may be adapting to changing environmental conditions. In particular, diet of the Meyer’s Parrot (*Poicephalus meyeri*) in Africa closely tracks fruiting phenology, suggesting that the species is an opportunistic generalist (Boyes and Perrin 2009).

Large-bodied parrot species consume predominantly seeds (Matuzak et al. 2008), and tend to exhibit a narrow dietary niche, concentrated on a few plant species (Renton et al. 2015). The Northern Mealy Amazon (*Amazona guatemalae*) is the largest Amazon parrot in continental America (38 cm; Forshaw 1989), and is considered Near Threatened (BirdLife International 2016). The species inhabits mainly tropical moist forest (Forshaw 1989), which is undergoing high rates of deforestation and conversion to secondary forest (de Jong et al. 2010). Little is known of the food resource requirements of the Northern Mealy Amazon, with only one report of the species consuming seeds of *Brosimum utile* in Costa Rica (Higgins 1979), and a list of 33 tree species consumed by Northern Mealy Amazons in Petén, Guatemala (Bjork 2004). Therefore, in the present study we aimed to determine dietary niche breadth of the Northern Mealy Amazon, and how this may vary with spatial-temporal variation in food resource availability in Los Chimalapas, Mexico. In this way, we proposed to evaluate whether parrots select food items in the diet, and elucidate potential foraging strategies employed by the Northern Mealy Amazon in a modified landscape.

Methods

Study area

We determined the diet of the Northern Mealy Amazon at three sites in Los Chimalapas, northeastern Oaxaca, Mexico (17°08'-17°04'N, 94°36'- 94°08'W). Annual rainfall in the region is between 2000-4500 mm, with mean annual temperatures of 22-26°C, and a short dry season from March to June (Trejo 2004). The dominant vegetation is tropical moist evergreen forest, which covers 45.7% of the landscape in Los Chimalapas (Martínez-Pacheco 2012). Common tree species in this vegetation are *Brosimum alicastrum*, *Dialium guianense, Terminalia Amazonia, Cojoba arborea* and *Calophyllum brasiliense*

(Rzedowsky 1978, Torres-Colín 2004). Riparian forest also occurs along permanent rivers in the lowlands, where dominant tree species are *Garcinia macrophylla, Inga vera*, *Vochysia guatemalensis* and *Ficus* spp., although this vegetation is surrounded by a matrix of areas converted to agriculture and cattle-grazing (Torres-Colín 2004). In recent decades, 2046.8 km^2 of primary forest have been converted by selective forestry and cattle-grazing (Martínez-Pacheco 2012), and most of these areas are occupied by grassland or secondary forest in different stages of succession. The northern region of Los Chimalapas, where the study was conducted, has suffered greatest impact from anthropogenic activities, and the area currently has an annual 5.8% rate of conversion of primary forest (Martínez-Pacheco 2012).

Food resource availability

We established 30 phenology transects (200 x 6 m) to determine food resource availability for parrots (Chapman et al. 1992), with 10 transects in each of three habitats: 1) tropical moist evergreen forest, 2) riparian forest, and 3) secondary forest of 15-25 years regeneration. We surveyed transects during the parrot breeding season (March-April 2014) and non-breeding season (August-September 2013) to record all fruiting trees with diameter at breast height (DBH) >10 cm. For each fruiting tree we measured tree DBH as an index of the biomass of fruits that may be produced by the tree (Chapman et al. 1994), and estimated the proportion of fruits in the tree canopy. We then calculated an index of fruit abundance for each tree by multiplying tree DBH with the proportion of canopy with fruits. For each transect, we considered the number of tree species fruiting, number of fruiting trees, and the sum of fruit abundance indices for each tree, as variables of food resource abundance that could be compared among habitats and seasons.

Diet of the Northern Mealy Amazon

We determined diet by direct observation of foraging parrots along survey routes in the same areas where phenology transects were conducted, during the months of March-May (breeding season), and August-October (non-breeding season). Each survey route was visited once a week during the first four hours of the morning (06:30-10:30; N = 432 h of observation), walking in one direction only, and at a constant pace, stopping only to record foraging parrots. We also recorded ad hoc observations of foraging parrots when these were encountered.

For each foraging record we noted: a) date and time, b) habitat, c) tree species, d) number of parrots, and e) plant part consumed (fruit, seed, flowers, leaves). We considered a foraging record as one or more parrots in a feeding tree, when the parrots moved to another resource, or tree, this was considered as a second foraging record (Galetti 1993, Renton 2001). Tree species were identified in the field, or by means of botanical samples collected for later identification at the National Herbarium of the Universidad Nacional Autónoma de México (MEXU) in Mexico City.

Statistical analyses

We used Shapiro-Wilk normality test on data from the phenology transects (Zar 1999). Data on number of fruiting trees in transects presented a normal distribution after log transformation, and complied with the Mauchly test of sphericity, therefore we applied two-way repeated measures ANOVA to determine spatial (habitats) and temporal (seasons) variation in resource availability. The other variables of species fruiting and index of fruit abundance only presented a normal distribution for data from the breeding season, therefore we applied one-way ANOVA to compare among habitats in the breeding season, and Kruskal-Wallis ANOVA to compare among habitats in the non-breeding season. Similarly, we applied Wilcoxon paired test to compare species and fruit abundance for each transect between seasons (Zar 1999). We applied post-hoc Tukey-Kramer (HSD) test to determine which group produced a significant difference among habitats (Zar 1999). We also calculated the Morisita index of similarity in abundance of fruiting trees for each tree species among the three forest types during the breeding season (Krebs 1999). Finally, we used chi-square contingency table to evaluate whether frequency of foraging by parrots and number of fruiting trees were associated with habitat.

We determined dietary niche-breadth of Northern Mealy Amazons by calculating Levins (1968) standardized niche index, using the number of parrots observed to consume each resource, where a niche index close to 0 indicates that parrots concentrate use on only a few of the resources, whereas a value close to 1 indicates that use is spread equally over the resources (Colwell and Futuyma 1971). We further evaluated resource selection in parrot diets by calculating the Hurlbet (1978) niche index that estimates niche-breadth considering the proportional use and availability of each resource. In this case, a value close to 0 indicates selection in the diet of resources with low availability, while a value close to 1 indicates that resources are consumed in accordance with their availability. We also applied chi-square test with simultaneous Bonferroni 95% confidence intervals to determine whether the use of resources in the diet differed significantly from that expected by their availability (Neu et al. 1974, Byers et al. 1984). We present descriptive statistics of means with standard deviation, and used a $P < 0.05$ significance level for statistical tests.

Results

Spatial-temporal variation in food resource availability

We registered a total of 217 fruiting trees of 39 species from 29 families in the phenology transects, where the families with greatest number of tree species fruiting were Bombacaceae, Leguminosae, Sapindaceae, Meliacacea and Elaeocarpaceae. During the breeding season the most abundant fruiting tree species were *Dialium guianense*, *Cecropia obtusifolia*, *Sloanea meianthera*, *Ficus* sp., *Cupania glabra* and *Schizolobium parahyba*, whereas during the non-breeding season *Guarea macrophylla*, *Quararibea funebris*, *Sloanea medusula* and *Cupania juglandifolia* were most abundant.

Two-way repeated measures ANOVA determined significant spatial and temporal variation in number of fruiting trees in phenology transects (Habitats: $F_{2,18} = 6.34$, $P = 0.008$; Seasons: $F_{1,9} = 31.07$, $P = 0.001$). Post-hoc test demonstrated that among habitats secondary forest had significantly fewer fruiting trees per transect (Fig. 1A) compared to primary evergreen ($F_{1,9} = 5.35$, $P = 0.046$) and riparian forest ($F_{1,9} = 11.73$, $P = 0.008$). Number of fruiting trees was also significantly lower in the non-breeding season compared to the breeding season (Fig. 1A). Finally, there was a significant interaction of habitat with season ($F_{2,18} = 5.24$, $P = 0.016$), where the difference among habitats in number of fruiting trees was greater during the breeding season than in the non-breeding season (Fig. 1A).

The same pattern of spatial and temporal variation was determined for number of tree species fruiting (Fig. 1B) and index of fruit abundance (Fig. 1C), which differed significantly among habitats in the breeding season (Species: $F_{2,29} = 7.9$, $P = 0.002$; Fruiting index: $F_{2,29} = 11.5$, $P < 0.001$). In both cases, Tukey-Kramer HSD post-hoc test demonstrated that secondary forest had significantly fewer species (Fig. 1B) and lower fruit abundance index (Fig. 1C) compared to riparian (Species: q =5.6, $P < 0.05$; Fruiting index: $q = 5.6$, $P = 0.002$), and evergreen forest (Fruiting index: $q = 6.1$, $P = 0.001$). By comparison, during the non-breeding season habitats did not differ significantly in number of tree species fruiting ($H_2 = 0.84$, $P = 0.65$) or fruit abundance index ($H_2 = 1.51$, $P = 0.47$).

The breeding season also had significantly more tree species fruiting (Wilcoxon Z = 4.5, $P < 0.001$; Fig. 1B), and a greater index of fruit abundance (Wilcoxon $Z = 4.8$, $P <$ 0.001; Fig. 1C) than the non-breeding season. This increased resource abundance during the breeding season was due mainly to fruiting of *Dialium guianense*, *Sloanea meianthera*, *Cecropia obtusifolia*, *Cupania glabra*, and *Ficus* sp. in primary forests, as well as *Hampea nutricia*, *Dialium guianense*, *Schizolobium parahyba*, *Ficus* sp., and *Alchornea latifolia* in secondary forest. Furthermore, during the breeding season composition of fruiting trees was similar between primary riparian and evergreen forest with a Morisita Index of 0.49, whereas secondary forest had a more distinct species composition of fruiting trees compared to riparian (Morisita = 0.28) and evergreen forest (Morisita = 0.25).

Diet of the Northern Mealy Amazon

We obtained a total of 82 foraging records of the Northern Mealy Amazon consuming fruits and seeds of 15 plant species from 14 families (Table 1). Seeds comprised the major portion of 82.9% of the diet, and these were mainly immature seeds (50% of the diet). Only 14.6% of foraging records represented the consumption of fruit by parrots, while we observed only one record each of parrots consuming leaves of the tree *Cupania glabra*, and wood of the tree *Schizolobium parahyba* (1.2% each; Table 1). Given that during the non-breeding season (Sep-Oct) very few parrots were present at the study site (De Labra-Hernandez and Renton *in rev*.), we only obtained three records of foraging by parrots on *Spondias mombin* (Anacardiaceae) during the non-breeding season. Therefore, all analyses of dietary niche and food resource selection were conducted only for data from the breeding season (March-May).

Considering the number of parrots using each food resource, we calculated an overall Levins´ niche breadth of $B = 0.513$ for Northern Mealy Amazon diets during the breeding season. This represents a broad niche breadth where use was spread relatively equally over the resources, with 8 plant resources contributing >5% of the diet (Fig. 2). Nevertheless, two plant species contributed over a third of parrot diets, with more parrots recorded consuming immature seeds of *Dialium guianense* (24.5%), and *Sloanea meianthera* (18%), which were the most abundant tree species recorded in fruiting phenology transects (Fig. 2).

Finally, chi-square contingency table found a significant association of frequency of parrot foraging records and number of fruiting trees by habitat ($\chi^2_2 = 6.7$, $P < 0.05$; Fig. 3). We obtained a greater number of foraging records of parrots in primary riparian (45 records; 56.9%) and evergreen forest (25 records; 31.7%), where there were also a greater number of fruiting trees, compared to secondary vegetation, with fewer foraging records (9 records; 11.4%) and fruiting trees (Fig. 3). Foraging flocks were also larger in primary forest with a mean 6.2 ± 5.1 parrots per foraging flock, compared to 3.7 ± 1.5 parrots per foraging record in secondary forest. Furthermore, when we calculated dietary niche breadth for parrots foraging in primary and secondary forest separately, we found a very broad niche breadth (Levins' $B = 0.888$; $N = 22$ parrots consuming 4 plant species) for parrots foraging in secondary forest, which was double that obtained for parrots foraging in primary forest (Levins' $B = 0.441$; $N = 178$ parrots consuming 14 plant species).

Food resource selection

Taking into consideration the proportional availability in phenology transects of each resource consumed in the diet of Northern Mealy Amazons during the breeding season, we obtained a broad Hurlbert's niche breadth of $Ha = 0.76$, indicating that resources were used in parrot diets according to their availability (Fig. 2). In general, use of resources by parrots in the diet did not differ significantly from that expected by resource availability ($\chi^2_{13} = 9.3$, $P = 0.75$), and the expected proportional use of each resource based on its availability did not fall outside the Bonferroni 95% confidence intervals for proportional use of that resource. This indicates that parrots do not exhibit selectivity of food resource items in the diet during the breeding season, but consume a number of food items in accordance with their availability. Hence, although *Dalium guianense* was the most consumed item in parrot diets, this was also the most abundant fruiting tree during the breeding season (Fig. 2).

Discussion

Temporal and spatial patterns of resource availability

Food resource availability for the Northern Mealy Amazon showed high temporal and spatial variability in the tropical moist forest of Los Chimalapas, Mexico. Most Central American forests, including tropical moist forests in Mesoamerica, present some dry months and demonstrate seasonality in fruiting phenology, with peak fruiting during the dry season (Corlett and Primark 2011, Morellato et al. 2013). The high seasonality we found in Los Chimalapas, with a marked decline in food resource availability during the rainy season, corresponds with that found by Bjork (2004) in the tropical moist forest of Petén, Guatemala, where there was a decline in food resource availability for the Northern Mealy Amazon during the non-breeding season.

In response to this seasonal decline in food resource availability, Bjork (2004) demonstrated that the Northern Mealy Amazon undertakes seasonal migrations of 50-95 km from the Petén in Guatemala to Lacandona in southeastern Mexico. In our study area of Los Chimalapas in northern Oaxaca, there is also a marked decline in abundance of Northern Mealy Amazons during the non-breeding, or rainy season (De Labra-Hernández and Renton *in rev*.). Our data on fruiting phenology demonstrate that this decline in parrot abundance corresponds with a marked decline in food resource availability during the non-breeding season. Such seasonal variations in food resource availability may be an precursor for the seasonal patterns of abundance and movements of species (Levey and Stiles 1992). Throughout the tropics, temporal and spatial variability in food resources influence patterns of abundance, movements, and habitat use by birds (Levey 1988, Loiselle and Blake 1991, Kinnaird et al. 1996, Mulwa et al. 2012), and other parrot species (Bonadie and Bacon 2000, Renton 2001, Symes and Perrin 2003, Berg et al. 2007, Ragusa-Neto 2007, 2008). Therefore it may be that Northern Mealy Amazons in Los Chimalapas are moving to alternate areas to track food resources during the non-breeding season.

At a spatial level among habitats, we found greater food resource availability for parrots in conserved primary forest vegetation, compared to secondary forest, particularly in the breeding season. Tropical moist forests are increasingly being converted to secondary forests (de Jong et al. 2010). As determined by our study, this conversion to secondary forest reduces food resource availability for primary forest species such as the Northern Mealy Amazon, which may have consequences for reproduction and productivity of threatened parrot species in tropical moist forest. In Australia, Carnaby's Cockatoo (*Zanda latirostris*) demonstrated a lower hatching success, nestling growth, and reproductive output in fragmented landscapes compared with birds breeding in areas of conserved forest (Saunders 1982, 1986, 1990), suggesting that cockatoo populations in fragmented landscapes were unable to obtain sufficient food resources to maintain the young during the breeding season. Therefore, conserving areas of primary tropical moist forest is essential to maintain food resource availability for threatened, forest-dependent, parrot species, such as the Northern Mealy Amazon, during the breeding season.

Parrot diet and resource use

The Northern Mealy Amazon consumed predominantly seeds of a variety of plant species. Therefore, as for other large-bodied Psitaciformes (Renton 2001, 2006, Matuzak et al. 2008, Boyes and Perrin 2009, Contreras-González et al. 2009), the Northern Mealy Amazon is primarily granivorous. However, contrary to the narrow dietary niche determined for other large-bodied psittacines during the breeding season (Renton 2001, 2006, Ragusa-Netto 2006, Matuzak et al. 2008, Contreras-González et al. 2009); the Northern Mealy Amazon demonstrated a broad dietary niche. We also found no evidence that the species selects food resources, but rather consumes food items in the diet according to their availability. We obtained a broad Hurlbert's niche breadth for the Northern Mealy

Amazon in the breeding season, which is similar to that found for other parrot species (Renton 2001, Díaz et al. 2012). Proportional use of each food resource in Northern Mealy Amazon diets during the breeding season also did not differ from that expected by availability. This contrast with the dietary selection demonstrated by the Ouvea Parakeet and the Military Macaw (*Ara militaris*) during the breeding season (Robinet et al. 2003, Contreras-González et al. 2009). However, the Ouvea Parakeet preferentially consumes food tree species that have some fruiting individuals throughout the year (Robinet et al. 2003), and the Military Macaw inhabited an extremely dry tropical forest with generally low food resource availability (Contreras-González et al. 2009).

Our results suggest that during the breeding season Northern Mealy Amazons have a broad diet, consuming a variety of resources according to their availability. Generalist feeding strategies are expected where resources are variable (MacArthur and Levins 1967, Schoener 1971), and means that parrots would not be dependent on the availability of a few key resources when raising young. Consuming a variety of items in the diet would provide opportunities for parrots to frequently sample different resources to detect changes in abundance (Clark and Mangel 1984). Rapid switching to newly available food resources was determined for the Meyer's Parrot in Africa (Boyes and Perrin 2009). This foraging strategy could be advantageous for parrots in that it enables rapid adaptation to variations in food resource abundance (Provenza and Cincotta 1993). This could permit greater plasticity in resource use by the Northern Mealy Amazon in the modified landscape of Los Chimalapas.

Foraging strategies of the Northern Mealy Amazon

We determined that frequency of foraging and abundance of fruiting trees were associated with forest type, where primary forest had more fruiting trees and greater frequency of foraging by parrots than secondary forest. This suggests that spatial heterogeneity in food resource abundance influences habitat use by the Northern Mealy Amazon. Habitat switching in accordance with food resource availability has been reported for other parrot species (Greene 1998, Renton 2001). Furthermore, when foraging in secondary vegetation foraging Northern Mealy Amazons consumed only a few plant species and presented a broad dietary niche breadth that was double the niche breadth of parrots foraging in primary forest. Therefore, Northern Mealy Amazons may adapt their dietary strategy according to the abundance of food resources.

The Northern Mealy Amazon demonstrated different foraging strategies in resource use at a both a temporal and spatial level. In response to the marked seasonal decline in food resource availability in Los Chimalapas during the non-breeding season, parrots could undertake migrations to alternative sites; as occurs in Petén, Guatemala (Bjork 2014). At a spatial level in Los Chimalapas during the breeding season parrots concentrated foraging activity in primary forest where more food resources were available, although some foraging occurred in secondary forest. Parrots also exhibited a broad dietary niche exploiting resources according to their availability. This suggests that parrots may be employing foraging strategies of sampling resource patches, and adjusting diet in response to variations in food resource abundance.

Acknowledgments

The study was conducted in partial fulfillment of a Ph.D. degree by MADLH at the Posgrado en Ciencias Biologicas, of the Universidad Nacional Autónoma de México (UNAM). Funding for the research was provided by the Programa de Apoyo a Proyectos de Investigación e Innovación Tecnológica (UNAM-DGAPA-PAPIIT grant IN205716) to KR. MADLH received a Doctoral studies grant from the Consejo Nacional de Ciencia y Tecnología (Conacyt 215549). We are grateful to Idea Wild who provided field equipment, and to Alvaro Campos who assisted with taxonomic identification of tree species. The Secretaria del Medio Ambiente y Recursos Naturales in Mexico provided research permits for the study. We are grateful to the authorities of the Santa Maria Chimalapa municipality for permission to work on their community lands, and to local people who provided assistance at field locations in San Francisco La Paz, San Antonio Nuevo Paraíso and Chalchijapa.

Literature cited

BIRDLIFE INTERNATIONAL [online]. 2016. *Amazona guatemalae*. <http://www.birdlife.org on 14/01/2016> (08 September 2016).

BJORK, R. 2004. Delineating patterns and process in tropical lowlands: Mealy Parrot migration dynamics as a guide for regional conservation planning. Ph.D. Dissertation, Oregon State University.

BONADIE, W. A., AND P. R. BACON. 2000. Year-round utilization of fragmented palm swamp forest by Red-bellied Macaws (*Ara manilata*) and Orange-winged Parrots (*Amazona amazonica*) in the Navira Swamp (Trinidad). Biological Conservation 95: 1–5.

BOYES, R. S., AND M. R. PERRIN. 2009. The feeding ecology of Meyer's Parrot *Poicephalus meyeri* in the Okavango Delta, Botswana. Ostrich 80: 153–164.

BULLOCK, S. H., AND J.A. SOLIS-MAGALLANES. 1990. Phenology of canopy trees of a tropical deciduous forest in Mexico. Biotropica 22: 22–35.

BYERS, C. R., R. K. STEINHORST, AND P. R. KRAUSMAN. 1984. Clarification of a technique for analysis of utilization-availability data. Journal of Wildlife Management 48: 1050–1053.

CHAPMAN, C. A., L. J. CHAPMAN, R. WRANGHAM, K. HUNT, D. GEBO, AND L. GARDNER. 1992. Estimators of fruit abundance of tropical trees. Biotropica 24: 527–531.

CHAPMAN, C. A., R. WRANGHAM, AND L. J. CHAPMAN. 1994. Indices of habitat-wide fruit abundance in tropical forests. Biotropica 26: 160–171.

CLARK, C. W., AND M. MANGEL. 1984. Foraging and flocking strategies: information in an uncertain environment. The American Naturalist 123: 626–641.

COLWELL, R. K., AND D. J. FUTUYMA. 1971. On the measurement of niche breadth and overlap. Ecology 52: 567–576.

CONTRERAS-GONZÁLEZ, A. M., F. A. RIVERA-ORTÍZ, C. SOBERANES-GONZÁLEZ, A. VALIENTE-BANUET, AND M. C. ARIZMENDI. 2009. Feeding ecology of Military Macaws (*Ara militaris*) in a semi-arid region of central Mexico. Wilson Journal of Ornithology 121: 384–391.

DE JONG, B., C. ANAYA, O. MASERA, M. OLGUIN, F. PAZ, J. ETCHEVERS, R. D. MARTINEZ, G. GUERRERO, AND C. BALBONTIN. 2010. Greenhouse gas emissions between 1993 and 2002 from land-use change and forestry in Mexico. Forest Ecology and Management 260: 1689‐1701.

DE LABRA-HERNÁNDEZ M. A., AND K. RENTON. En rev. Factors influencing density of the Northern Mealy Amazon in three forest types of a modified rainforest landscape in Mesoamerica. Avian Conservation and Ecology.

DÍAZ, S., T. KITZBERGER, AND S. PERIS. 2012. Food resources and reproductive output of the Austral Parakeet (*Enicognathus ferrugineus*) in forest of northern Patagonia. Emu 112: 234–243.

FORSHAW, J. M. 1989. Parrots of the world. Australia: Landsdown Editions.

GALETTI, M. 1993. Diet of the Scaly-headed Parrot (*Pionus maximiliani*) in a semi-deciduous forest in southeastern Brazil. Biotropica 25: 419–425.

GREENE, T. C. 1998. Foraging ecology of the Red-crowned Parakeet (*Cyanoramphus novaezelandiae novaezelandiae*) and Yellow-crowned Parakeet (*C. auriceps auriceps*) on Little Barrier Island, Hauraki Gulf, New Zealand. New Zealand Journal of Ecology 22: 161–171.

HIGGINS, M. L. 1979. Intensity of seed predation on *Brosimum utile* by Mealy Parrots (*Amazona farinosa*). Biotropica 11: 80.

HURLBERT, S. H. 1978. The measurement of niche overlap and some relatives. Ecology 59: 67–77.

JOHNSON, M. D. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65–71.

JONES, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk 118: 557–562.

KREBS, C. J. 1999. Ecological methodology. 2nd ed. Addison-Welsey. Educational Publishers Inc Menlo Park, California, USA.

LEVEY, D. J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. Ecological Monographs 58: 251–269.

LEVEY, D. J., AND F.G. STILES. 1992. Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. The American Naturalist 140: 447–476.

LEVINS, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, NJ.

LOISELLE, B. A., AND J. G. BLAKE. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology 72: 180–193.

MACARTHUR, R. H., AND E. R. PIANKA. 1966. On optimal use of a patchy environment. The American Naturalist 100: 603–609.

MACARTHUR, R., AND R. LEVINS. 1967. The limiting similarity, convergence, and divergence of coexisting species. The American Naturalist 101: 377–385.

MARTÍNEZ-PACHECO, A. I. 2012. Monitoreo del cambio de uso de suelo en Los Chimalapas 2000-2003. In: Una mirada desde el corazón de la jícara de oro. Experiencias de conservación en la Selva Zoque de Los Chimalapas (D. Ortega del Valle, T. Carranza-López, and J. Martínez-Pérez, eds.), pp. 86-94. WWF-México Oaxaca, México.

MATUZAK, G. D., M. B. BEZY, AND D. J. BRIGHTSMITH. 2008. Foraging ecology of parrots in a modified landscape: seasonal trends and introduced species. Wilson Journal of Ornithology 120: 353–365.

MORELLATO, L. P.C., M. G. G. CAMARGO, AND E. GRESSLER. 2013. A review of plant phenology in South and Central America. In: Phenology: an interactive environmental science (M. D. Schwarts, ed.), pp. 91–113. 2nd edn. New York, Springer.

MULWA, R. K., E. L. NEUSCHULZ, K. BÖHNING-GAESE, AND M. SCHLEUNING. 2012. Seasonal fluctuations of resource abundance and avian feeding guilds across forest–farmland boundaries in tropical Africa. Oikos 122: 524–532.

NEU, C. W., C. R. BYERS, AND J. M. PEEK. 1974. A technique for analysis of utilization-availability data. Journal of Wildlife Managements 38: 541–545.

PROVENZA, F. D., AND R. P. CINCOTTA. 1993. Foraging as a self-organizational learning process: accepting adaptability at the expense of predictability. In: Diet selection: an interdisciplinary approach to foraging behavior (R. N. Hughes ed.), pp 78–101. Blackwell Scientific Publications, Oxford.

PYKE, G. H., H. R. PULLIAM, AND E. L. CHARNOV. 1997. Optimal foraging: a selective review of theory and test. Quarterly Review of Biology 52: 137–154.

RAGUSA-NETTO, J. 2006. Dry fruits and the abundance of the Blue-and-yellow Macaw (*Ara ararauna*) at cerrado remnant in central Brazil. Ornitologia Neotropical 17: 491–500.

RAGUSA-NETTO, J. 2007. Nectar, fleshy fruits and the abundance of parrots at a gallery forest in the southern Pantanal (Brazil). Studies on Neotropical Fauna and Enviroment 42: 93–99.

RAGUSA-NETTO, J. 2008. Yellow-chevroned Parakeet (*Brotogeris chiriri*) abundance and canopy foraging at a dry forest in western Brazil. Studies on Neotropical Fauna and Enviroment 43: 99–105.

RENTON, K. 2001. Lilac-crowned parrot diet and food resource availability: resource tracking by a parrot seed predator. Condor 103: 62–69.

RENTON, K. 2006. Diet of adult and nestling Scarlet Macaws in southwest Belize, Central America. Biotropica 38: 280–283.

RENTON, K., A. SALINAS-MELGOZA, M. A. DE LABRA-HERNÁNDEZ, AND S. M. DE LA PARRA-MARTÍNEZ. 2015. Resource requirements of parrots: nest site selectivity and dietary plasticity of Psittaciformes. Journal of Ornithology 156:S73–S90 doi: 10.1007/s10336-015-1255-9.

ROBINET, O., V. BRETAGNOLLE, AND M. CLOUT. 2003. Activity patterns, habitat use, foraging behavior and food selection of the Ouvea Parakeet (*Eunymphicus cornutus uvaeensis*). Emu 103: 71–80.

RZEDOWSKY, J. 1978. Vegetación de México. Editorial Limusa, Mexico City. Mexico.

SAUNDERS, D. A. 1982. The breeding behavior and biology of the short-billed form of the White-tailed Black Cockatoo *Calyptorhynchus funereus*. Ibis 124: 422–455.

SAUNDERS, D. A. 1986. Breeding season, nesting success and nestling growth in Carnaby’s Cockatoo, *Calyptorhynchus funereus latirostris*, over 16 years at Coomallo Creek, and a method for assessing the viability of population in other areas. Aust. Wild. Res. 13:261–73.

SAUNDERS, D. A. 1990. Problems of survival in an extensively cultivated landscape: the case of Carnaby’s Cockatoo *Calyptorhynchus funereus latirostris*. Biological Conservation 54: 277–290.

SCHOENER, T.W. 1971. Theory of feeding strategies. Annual Review of Ecology and Systematics 2: 369–404.

SYMES, C. T., AND M. R. PERRIN. 2003. Seasonal occurrence and local movements of the Grey-headed (Brown-necked) Parrot *Poicephalus fuscicollis suahelicus* in southern Africa. African Journal of Ecology 41: 299–305.

TREJO, I. 2004. Clima. In: Biodiversidad de Oaxaca (A. J. García-Mendoza, M. J. Ordoñez, and M. Briones-Salas, eds.), pp 67–85. Instituto de Biología, UNAM, Fondo Oaxaqueño para la Conservación de la Naturaleza, WWF-México, Mexico City. Mexico.

Torres-Colín, R. 2004. Tipos de vegetación. In: Biodiversidad de Oaxaca (A. J. García-Mendoza, M. J. Ordoñez, and M. Briones-Salas, eds.), pp 105–117. Instituto de Biología, UNAM, Fondo Oaxaqueño para la Conservación de la Naturaleza, WWF-México, Mexico City. Mexico.

WHITE, L. J. T. 1994. Patterns of fruit-fall phenology in the Lopé Reserve, Gabon. Journal of Tropical Ecology 10: 298–312.

ZAR, J. H. 1999. Biostatistical analysis. 4th edition. Prentice Hall Inc New Jersey, USA.

Table 1. Diet observations of the Northern Mealy Amazon in tropical moist forest of Los Chimalapas, Mexico.

Plant species / Family	Plant part consumed	Feeding records	N° parrots	Months
Spondius mombin Anacardiaceae	Fruit	3	18	September
Cymbopetalum baillonii Annonaceae	Immature seeds	2	6	April
Dialium guianense Caesalpinioideae	Immature and mature seeds	16	49	April-May
Schizolobium parahyba Leguminosae	Immature seeds, Wood	8	16	March-April
Garcinia macrophylla Clusiaceae	Immature seeds	3	6	May
Sloanea meianthera Elaeocarpaceae	Immature seeds	13	36	March-May
Terminalia amazonia Combretaceae	Immature seeds	1	3	May
Alchornea latifolia Euphorbiaceae	Immature and mature seeds	4	11	April-May

Vatairea lundelii Leguminosae	Immature seeds	9	19	April-May
Lacistema aggregatum Lacistemataceae	Mature seeds	5	10	March-April
Guarea grandifolia Meliaceae	Mature seeds	2	5	April
Ficus sp. Moraceae	Fruit	7	21	April-May
Cupania glabra Sapindaceae	Mature seeds, Leaves	5	10	April-May
Pouteria sapota Sapotaceae	Fruit	2	4	April
Cecropia obtusifolia Urticaceae	Mature seeds	2	4	May
Cymbopetalum baillonii Annonaceae	Immature seeds	2	6	April

Figure legends

Fig. 1. Food resources availability during the breeding and non-breeding season of the Northern Mealy Amazon for (A) number of fruiting trees, (B) number of species fruiting, and (C) index of fruit abundance ($\sum$dbh x proportion canopy with fruits), in three vegetation types of Los Chimalapas, Mexico. Dissimilar letters above bars denote significant differences among habitats (Tukey–Kramer HSD test, $P < 0.05$).

Fig. 2. Proportional use and availability of fruiting tree species consumed by the Northern Mealy Amazon during the breeding season in Los Chimalapas, Mexico.

Fig. 3. Proportion of fruiting trees and Northern Mealy Amazon foraging records during the parrot breeding season, in three forest types of tropical moist forest in Los Chimalapas, Mexico.

Fig. 1

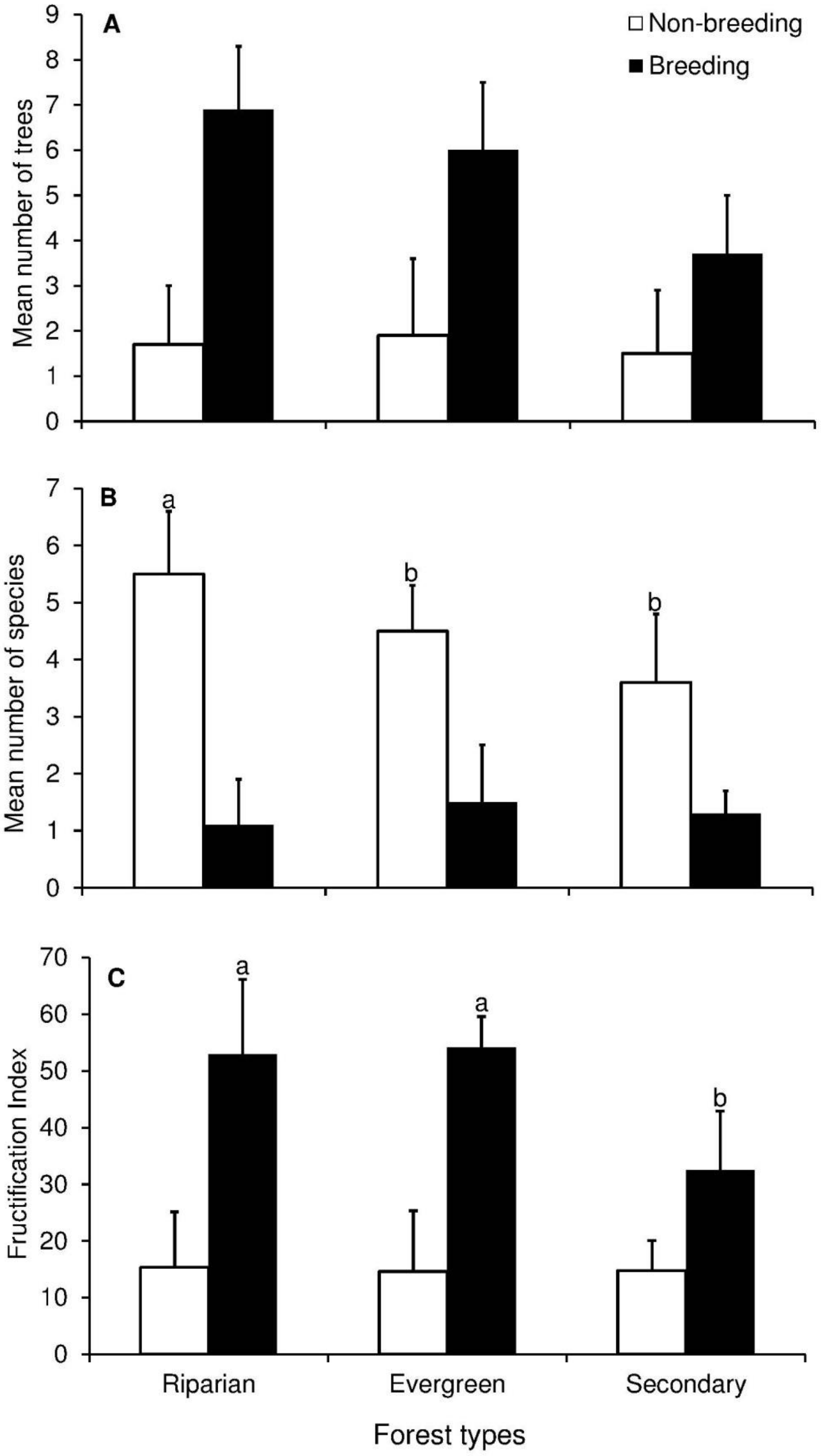

A
□ Non-breeding
■ Breeding
Mean number of trees
0
1
2
3
4
5
6
7
8
9
B
Mean number of species
0
1
2
3
4
5
6
7
a
b
b
C
Fructification Index
0
10
20
30
40
50
60
70
a
a
b
Riparian
Evergreen
Secondary
Forest types

Fig. 2

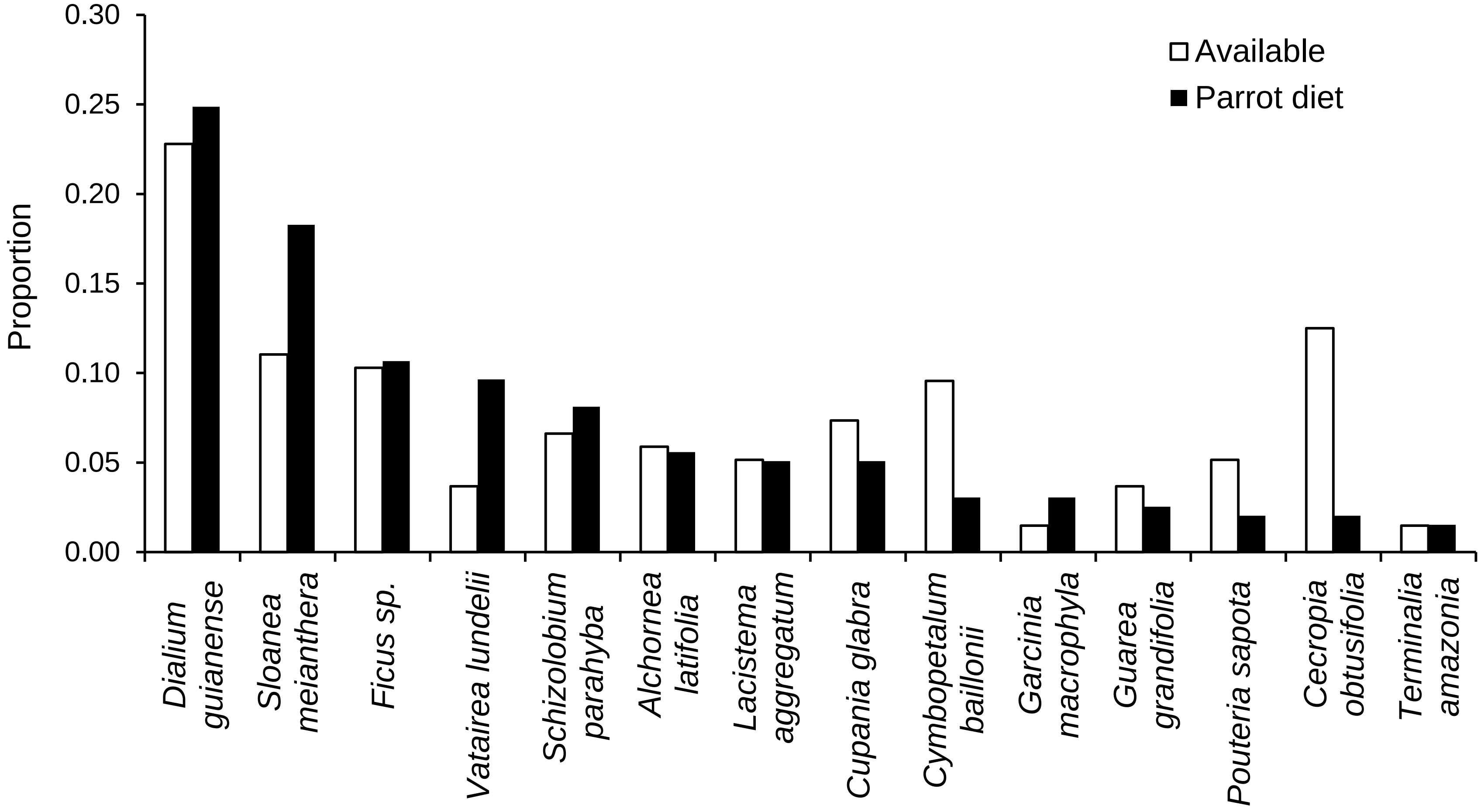
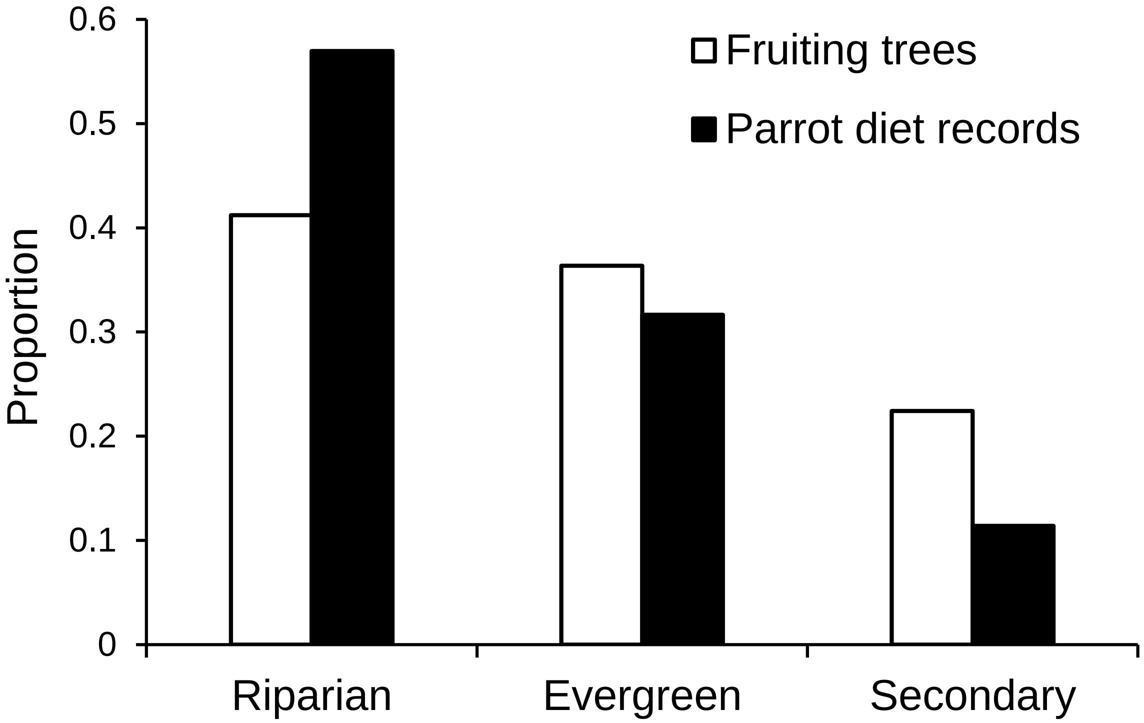

0.30
0.25
0.20
0.15
0.10
0.05
0.00
Proportion
□ Available
■ Parrot diet
Dialium guianense
Sloanea meianthera
Ficus sp.
Vatairea lundelii
Schizolobium parahyba
Alchornea latifolia
Lacistema aggregatum
Cupania glabra
Cymbopetalum baillonii
Garcinia macrophyla
Guarea grandifolia
Pouteria sapota
Cecropia obtusifolia
Terminalia amazonia

Fig. 3



0.6
0.5
0.4
0.3
0.2
0.1
0
Proportion
☐ Fruiting trees
■ Parrot diet records
Riparian
Evergreen
Secondary

CAPÍTULO IV

(Manuscrito redactado)

Factores que influyen en la reproducción y abundancia del loro corona azul (*Amazona guatemalae*) bajo un modelo de distribución libre ideal en un paisaje modificado

Miguel Ángel De Labra-Hernández[1] y Katherine Renton[2]*

[1]Posgrado en Ciencias Biológicas, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico City, Mexico.

[2]Estación de Biología Chamela, Instituto de Biología, Universidad Nacional Autónoma de México, Apartado Postal 21, San Patricio-Melaque, Jalisco, Mexico.

*Corresponding Author: K. Renton (krenton@ib.unam.mx)
Telephone & Fax: 52-315-3510202

Estado del proceso: ***Artículo redactado***

Resumen

A pesar de que el loro *Amazona guatemalae*, se encuentra casi amenazado a nivel internacional, no se conocen su productividad reproductiva en vida silvestre, o si se dispersa hacia los sitios de mejor calidad al seguir un modelo de distribución libre ideal, con beneficios en el éxito reproductivo. Durante un periodo de 4 temporadas reproductivas, evaluamos la productividad y supervivencia de nidos del loro corona azul en Los Chimalapas, al sureste de México. Además, determinamos si la disponibilidad de recursos se relaciona con la abundancia de los loros al seguir un modelo de distribución libre ideal y el potencial efecto sobre el éxito reproductivo. Los resultados demuestran que la productividad y el éxito de anidación de *A. guatemalae* son bajos. El fracaso en los nidos se debe principalmente por la captura de los pollos, donde los nidos ubicados a mayor distancia de los poblados tienen mayor probabilidad de éxito. Se comprobó que la abundancia de loros está relacionada con la disponibilidad de recursos, y sigue un modelo de distribución libre ideal, al ser proporcional a la disponibilidad de recursos en cada hábitat. Cabe destacar que la captura de pollos podría tener un efecto indirecto en la adecuación del loro corona azul y finalmente en su permanencia a largo plazo. Los planes de conservación deben estar dirigidos en evitar la captura ilegal.

Palabras claves: Psitaciformes, tráfico ilegal, éxito reproductivo, Distribución Libre Ideal, Mesoamérica.

Introducción

En hábitats heterogéneos o modificados, los individuos deben distribuirse y elegir los parches de mayor disponibilidad de recursos (MacArthur and Pianka 1966), con el propósito de garantizar el éxito reproductivo. La teoría de la distribución libre ideal (Fretwell y Lucas 1969) predice que la distribución de los individuos entre hábitats debe ser proporcional a la disponibilidad de los recursos, donde los individuos deberían elegir el hábitat de mejor calidad (mayor disponibilidad de recursos) con beneficios en su supervivencia y reproducción (Fretwell y Lucas 1969, Cody 1985, Jones 2001). Sin embargo, cuando la densidad de individuos en un hábitat aumenta, la adecuación disminuye por efecto de la competencia, por lo cual los individuos podrían utilizar otros hábitats y presentar selección denso-dependiente del hábitat (Rosenzweig 1985, 1991). No obstante, se esperaría que los individuos que utilicen los hábitats de menor calidad y disponibilidad de recursos, sean menos abundantes, y presenten menor éxito reproductivo.

Para varias especies de psitácidos es insuficiente el conocimiento de los requerimientos ecológicos, uso y selección del hábitat, con la mayoría de los estudios en psitácidos insulares de Asia (Marsden y Royle 2015). Dichos estudios demuestran diferencias en la abundancia de psitácidos entre hábitats primarios, mientras que en hábitats degradados presentan menores abundancias (Marsden y Royle 2015). En particular, los estudios de uso del hábitat realizados en las islas de Indonesia indican que las cacatúas de talla grande, presentan mayor densidad en bosques conservados con mayor cobertura arbórea (Marsden 1992, Marsden y Fielding 1999, Kinnaird et al. 2003). En particular, los hábitats primarios presentan mayor disponibilidad de recursos potenciales para la anidación, por lo tanto, la densidad de cacatúas parece estar asociada con la densidad de sitios potenciales de anidación en los bosques primarios (Kinnaird et al. 2003, Marsden y Pilgrim 2003). Asimismo, se ha observado para varias especies de psitácidos fluctuaciones en su abundancia asociado con variaciones en la disponibilidad de los recursos alimenticos (Beeton 1985, Wirminghaus et al. 2001, Ragusa-Neto 2004, 2007, Karubian et al. 2005, Manning et al. 2007, Rivera-Ortiz et al. 2008). Por esta razón, la distribución y abundancia de los psitácidos podría seguir un modelo de distribución libre ideal, aunque esto no ha sido directamente comprobado en los estudios de psitácidos.

Únicamente, en un estudio de la reproducción del perico *Forpus passerinus* en Venezuela, Bonebrake y Beissinger (2010) determinaron que existe variación entre sitios de anidación respecto a la cobertura de la vegetación, y que ésta característica de la estructura del hábitat influye en la productividad reproductiva de los nidos. Además, indican que los pericos se mueven hacia los hábitats de mayor calidad cuando tienen oportunidad de cambiar el sitio de anidación. Por lo que, Bonebrake y Beissinger (2010) sugieren que los pericos pueden evaluar la calidad del sitio de anidación mediante la cobertura de la vegetación y dispersarse hacia los sitios de mejor calidad con beneficios en el éxito reproductivo, al seguir un modelo libre ideal. Sin embargo, aún falta determinar si la abundancia de los psitácidos entre hábitats es proporcional a la disponibilidad de los recursos y si los psitácidos seleccionan los hábitats de mejor calidad para su adecuación.

Por lo tanto, en el presente estudio se propone determinar si el loro corona azul sigue un modelo de distribución libre ideal que influye sobre su éxito reproductivo. Como hipótesis, consideramos que la abundancia de loros en los hábitats debe ser proporcional a la disponibilidad de recursos alimenticios y sitios de anidación. Asimismo, consideramos que los loros deben de elegir mediante la distribución libre ideal los hábitats de mejor calidad que benefician su éxito reproductivo. Por lo tanto, los objetivos específicos del estudio son: 1) determinar si la abundancia del loro se relaciona con la disponibilidad de recursos, 2) evaluar el desempeño reproductivo del loro al considerar el tamaño de puesta, el éxito de eclosión y la supervivencia de los pollos, y 3) comprobar si la distribución del loro entre los hábitats sigue un modelo libre ideal al relacionar la disponibilidad de recursos con la abundancia de los loros y el potencial efecto en su éxito reproductivo.

Métodos

Sitios de muestreo

El estudio se realizó en la región de Los Chimalapas, al sureste de México, en cuatro sitios: Chalchijapa (17° 03' 15"N; 94° 39' 23"E), San Antonio (17° 09' 38"N; 94° 21 '9" E), San Francisco (17° 05' 44.5"N; 94° 07' 8.4" E), y La Fortaleza (17° 09' 32.2"N; 94° 13' 45.3" E). En la región, la temperatura promedio anual es de 22-26°C, con un total de precipitación anual que varía entre 2,000-4,500 mm, con una corta estación seca de marzo a junio (Trejo 2004). Dentro de la región, se establecieron 12 rutas de muestreo, con 4 rutas de muestreo en cada uno de tres tipos de vegetación: bosque tropical perennifolio, bosque ribereño a lo largo de ríos permanentes, y áreas degradadas con vegetación secundaría. En cada ruta de muestreo, se llevaron a cabo puntos de conteo de radio variable (Capítulo I) para determinar la abundancia de los loros. Asimismo, se establecieron transectos de fenología (200 x 6 m) para determinar la disponibilidad de recursos alimenticos (Capítulo III), así como parcelas de 1 ha donde se llevó a cabo censos de cavidades de árboles (Capítulo II). Por último, en los mismos sitios se realizaron búsquedas de nidos del loro corona azul.

Búsqueda y revisión de nidos del loro corona azul

Durante la temporada reproductiva de marzo-mayo en 2013-2016, se dio seguimiento a los nidos del loro corona azul para determinar su productividad y éxito reproductivo. Se localizaron los nidos de los loros al monitorear el comportamiento de las parejas reproductivas, y con la ayuda de guías locales. La revisión de cada nido se realizó utilizando la técnica de escalada con una cuerda (*single-rope climbing*; Houle et al. 2004). Hasta donde fue posible, cada nido se visitó semanalmente para obtener los parámetros reproductivos de tamaño de puesta, eclosión, tamaño de nidada y número de pollos en etapa tardía (> 30 días de edad).

Evaluación del hábitat de anidación

Para cada nido registrado se midieron distintas variables a nivel de la cavidad, sitio de anidación y paisaje, que pueden estar relacionadas con la supervivencia de los nidos. Respecto a la cavidad, se consideraron las variables de altura desde el suelo, profundidad y diámetro interno; características que el loro selecciona para anidar (Capítulo II). Para evaluar el hábitat del sitio de anidación, se estableció una parcela de 25 m de radio alrededor de cada nido de loro encontrado. En esta parcela, se clasificó el estado de conservación del hábitat donde el nido fue ubicado, como nido dentro del bosque primario conservado o en áreas alteradas de vegetación secundaria o pastizal. Asimismo, se estimó el porcentaje de cobertura del dosel y se obtuvo el número de árboles dentro de cada parcela alrededor del nido. Las variables a nivel del paisaje, se obtuvieron al medir la distancia del nido al borde del bosque, y la distancia del nido al asentamiento humano más cercano mediante el programa Google Earth.

Abundancia de loros y disponibilidad de recursos

De los loros registrados mediante los puntos de conteo, se consideró el promedio del número de loros/punto de conteo en cada ruta de monitoreo (5.2 ± 1.6 puntos de conteo / ruta, *n* = 12 rutas). Asimismo, para cada ruta de monitoreo se obtuvo el promedio del índice de fructificación (∑ dap árbol x proporción de copa con frutos) generado con los transectos de fenología (2.5 ± 0.5 transectos / ruta, *n* = 12 rutas). Por último, se consideró la abundancia de cavidades accesibles para la anidación de los loros (Capítulo II) por hectárea de muestreo cercano a las rutas de monitoreo (2 parcelas / ruta). La densidad de cavidades accesibles se obtuvo al considerar mediciones hechas a 5 ejemplares del loro corona azul depositados en la Colección Nacional de Aves del Instituto de Biología de la UNAM (tamaño entre el dorso y el pecho = 7.5 ± 0.2 cm; rango 7.3–7.8 cm). Así, consideramos únicamente como cavidades accesibles para la anidación del loro aquellas con diámetro de entrada >7 cm (Capítulo II).

Adicionalmente, para conocer los recursos alimenticios utilizados para la alimentación de las crías de los loros, se tomaron muestras de buche de los pollos (>30 días de edad) siguiendo las recomendaciones de Enkerlin-Hoeflich et al. (1999). Cada muestra fue colocada individualmente en una bolsa hermética y fue marcada con código del nido, fecha, y número de la cría por orden de eclosión. Posteriormente, cada componente de la muestra fue separado según el tipo, forma, tamaño y color, y fue identificado por comparación de muestras colectadas en campo y por la información de forrajeo de los adultos (Capítulo III). Los componentes fueron contabilizados y pesados con ayuda de una balanza electrónica calibrada a 0.001g para determinar la frecuencia de ocurrencia y el porcentaje de biomasa agrupado por nido.

Análisis estadístico

Éxito reproductivo. Para determinar los factores que tienen mayor influencia en la supervivencia de los nidos aplicamos modelos lineales generalizados mixtos (GLMM), con el uso del comando glmer (paquete lmer4) y la función de enlace "logexp" (*logistic-exposure*; Schaffer 2004) en R 3.2.3 (R Core Team, 2015). En los modelos, se consideró como variable respuesta el resultado del nido: éxito = 1, o fracaso = 0. Se consideró como exitoso aquel nido que contenía pollos en la etapa tardía durante el último día de observación.

Para la construcción de los modelos se consideraron 8 factores fijos, incluyendo las tres variables de la cavidad (altura del suelo, profundidad y diámetro interno), tres variables del hábitat, siendo el estado del hábitat (primario/modificado) donde se ubicaron los nidos, el % de cobertura del dosel, la densidad de árboles alrededor del nido (0.02 ha), y las variables del paisaje de distancia del nido al borde del bosque, y la distancia del nido al poblado. Asimismo, se consideraron como factores aleatorios el código del nido (ID) y el año, con el propósito de reducir sesgos por la reutilización de una cavidad como sitio de anidación por los loros en diferentes años, y controlar las posibles variaciones interanuales de la supervivencia. En total se generaron 8 modelos, incluyendo el modelo nulo sin los efectos fijos (parámetros) para comparar con los modelos incluyendo los parámetros, el modelo global con efecto de todos los parámetros, y 6 modelos reducidos que se generaron removiendo secuencialmente los efectos fijos con el uso del método "drop1" (Zuur et al.

2009). El mejor modelo se seleccionó mediante el Criterio de Información de Akaike corregido para muestras pequeñas (AICc; Burnham y Anderson 2002). Además se calculó el delta de Akaike (Δ AICc) para conocer las diferencias relativas entre los valores de AICc, así como el peso de Akaike (*wi*) para conocer la probabilidad que tienen cada modelo de ser el que mejor explique el efecto sobre la variable respuesta.

Para calcular la tasa de supervivencia diaria de los nidos de los loros, se utilizaron los resultados del mejor modelo, que indica los factores que influyen en la supervivencia. De esta forma la tasa de supervivencia se calculó con base en Schaffer (2004):

$$\mathrm{DSR} = \frac{e^{\beta_0 + \beta_1 x}}{1 + e^{\beta_0 + \beta_1 x}}$$

dónde: DSR es la tasa de supervivencia diaria, β_0 es el valor del intercepto calculado por el mejor modelo para el parámetro por separado, β_1 es el valor de la pendiente del parámetro y x es cada valor de la variable independiente. Se consideró un periodo de 78 días de duración del nido del loro corona azul con base en nuestras observaciones e información de la literatura (Bjork 2004). Así, la tasa finita de supervivencia de los nidos se estimó al elevar el exponente la tasa de supervivencia diaria por el número de días requeridos desde la etapa de incubación hasta la etapa de volantón (DSR^{78} en el caso del loro corona azul).

Relación entre abundancia de loros y recursos alimenticios

Para comprobar la relación de la abundancia del loro en cada sitio con la disponibilidad de recursos, se aplicaron modelos lineales generalizados (GLM) con errores de tipo Poisson y función de enlace “log” en R 3.2.3 (R Core Team, 2015). En los modelos se incluyó como variable respuesta el promedio de abundancia de loros/punto conteo generada para cada una de las 12 rutas de muestreo. Mientras que las variables independientes fueron el promedio del índice de fructificación y la densidad de cavidades accesibles por ruta de muestreo.

Resultados

Reproducción del loro corona azul

Se observaron eventos de cópula de las parejas de loros durante la tercer y cuarta semana de marzo (*n* = 10 parejas). La puesta de huevos ocurrió durante un periodo de un mes, con el primer registro el 24 de marzo (*n* = 2 nidos) y el último registro 31 días después (*n* = 2 nidos). Sin embargo, el pico de registros de nidos con huevos ocurrió durante la segunda y tercer semana de abril. Los primeros registros de eclosión ocurrieron durante la primer semana de abril (06 de abril 2014; *n* = 1 nido) y hasta la tercera semana de mayo (19 mayo 2014; *n* = 1 nido), con el mayor número de nidos con pollos registrados durante la cuarta semana de abril y la primera semana de mayo (*n* = 12 nidos). Los pollos que llegaron a una etapa tardía (>30 días después de la eclosión) se registraron entre el 8-21 de mayo de cada temporada (*n* = 20 pollos con más de 5 semanas de edad). Con esta información, se estimó que el periodo reproductivo del loro corona azul inicia de febrero-marzo, con la búsqueda de nidos y cópula, hasta finales de junio y principios de julio con la salida de volantones (Figura 1).

Figura 1. Periodo reproductivo del loro corona azul en la región de Los Chimalapas durante el 2013–2016.

Productividad reproductiva

Entre 2013-2016, obtuvimos información para 48 nidos del loro corona azul, con el mayor número de huevos y pollos eclosionados para el año 2016 (Tabla 1). Registramos un total de 123 huevos (todos los nidos) y un promedio de tamaño de puesta de 2.6 ± 0.6 huevos (rango 1 – 4 huevos; figura 2a). En general el tamaño de puesta más frecuente fue de 3 huevos, y únicamente para el año 2014 se registró un nido con 4 huevos. Respecto al número de pollos eclosionados, registramos un promedio de 1.7 ± 0.9 en 38 nidos que llegaron a esta etapa (rango 1 – 3 pollos; figura 2b), y en general registramos 2 pollos eclosionados por nido. Considerando el último día de observación de los nidos con pollos, en 9 nidos se registraron en promedio 0.5 ± 0.9 pollos con una edad tardía >30 días (rango 2 – 3 pollos; Figura 2c). Por ello, mientras el tamaño de puesta más frecuente fue de 3 huevos, el tamaño de nidada más frecuente fue de 2 pollos eclosionados (Figura 2).

Sin embargo, los nidos con 3 huevos fueron más productivos resultando en un promedio de 0.6 ± 1.1 pollos tardíos (rango 2 – 3 pollos; *n* = 15 pollos), mientras los nidos con 2 huevos produjeron en promedio 0.4 ± 0.6 pollos tardíos (rango 1 – 2 pollos; *n* = 5 pollos). En general, al inicio de la temporada, las hembras ponen un promedio de 2.6 huevos / hembra, y eclosionan 1.7 pollos / hembra, pero al final solo llegan 0.5 pollos tardíos / hembra. La mayor pérdida en la productividad ocurre durante la etapa de crianza de los pollos dado que el 61.7% de los huevos logran eclosionar, pero tan solo 16.3% de los pollos eclosionados llegan a la etapa de pollo tardío.

La principal causa del fracaso en los nidos del loro corona azul fue el saqueo de los pollos (57.1%; Figura 3). En total se saquearon 24 pollos de los nidos, con el mayor número de pollos capturados durante el año 2016 (66.7%, *n* = 16 pollos). Asimismo, la depredación natural también afecta en mayor porcentaje durante la etapa de pollo (28.6%; Figura 3).

Tabla 1. Productividad reproductiva del loro corona azul por hembra en la región de Los Chimalapas durante el 2013-2016.

Parámetros	2013	2014	2015	2016	2013-2016
Número de nidos	3	18	13	14	48
Número de huevos	7	41	36	39	123
Tamaño puesta (promedio ± SD)	2.3 ± 1.2	2.4 ± 0.7	2.8 ± 0.4	2.8 ± 0.4	2.6 ± 0.6
Numero de eclosiones	ND	28	22	26	76
Pollos eclosionados por hembra (promedio ± SD)	ND	1.6 ± 0.9	1.7 ± 1.2	1.9 ± 0.5	1.7± 0.9
Número pollos tardíos	ND	9	5	6	20
Pollos tardíos por hembra (promedio ± SD)	ND	0.6 ± 1	0.4 ± 0.9	0.4 ± 0.9	0.5 ± 0.9

Figura 2. Distribución relativa del (a) tamaño de puesta, y (b) número de pollos eclosionados, y (c) número de pollos en etapa tardía (>30 días de edad) de los nidos registrados para el loro corona azul durante el 2013–2016. Los números sobre cada barra corresponde al tamaño de muestra (nidos).

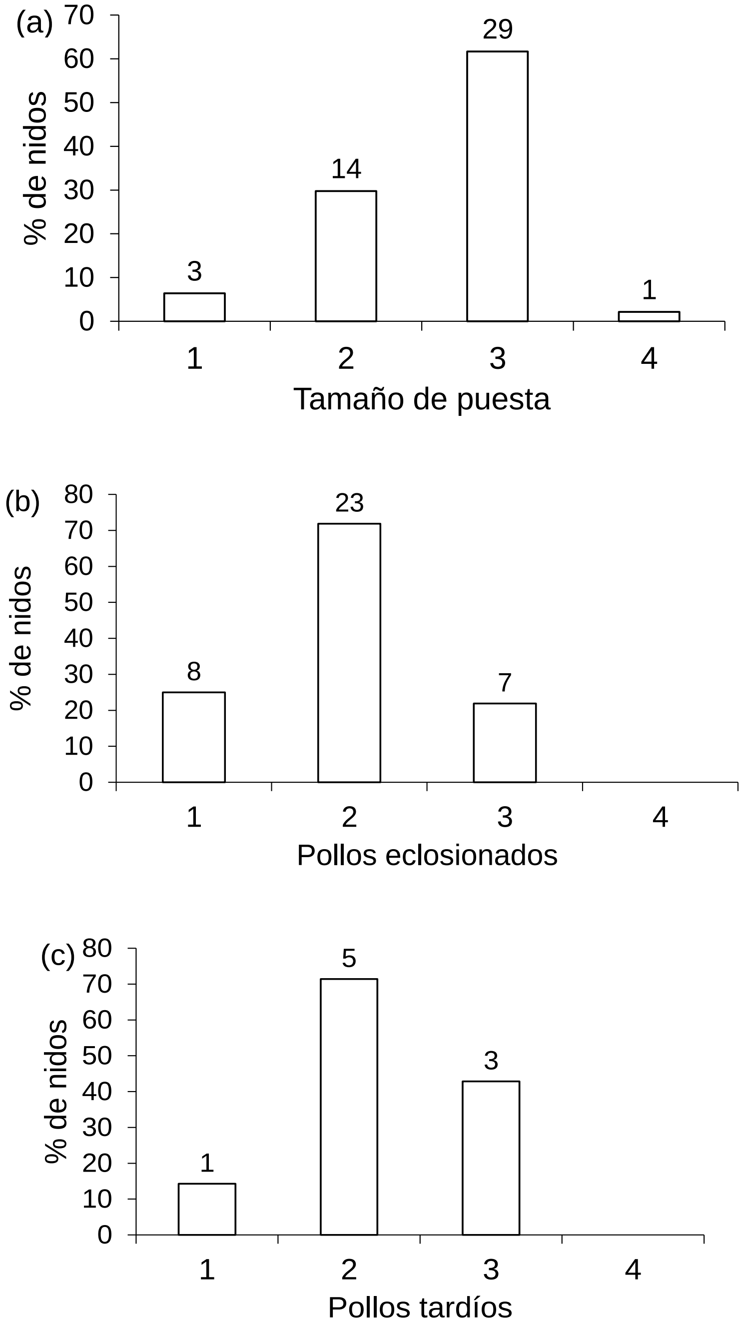
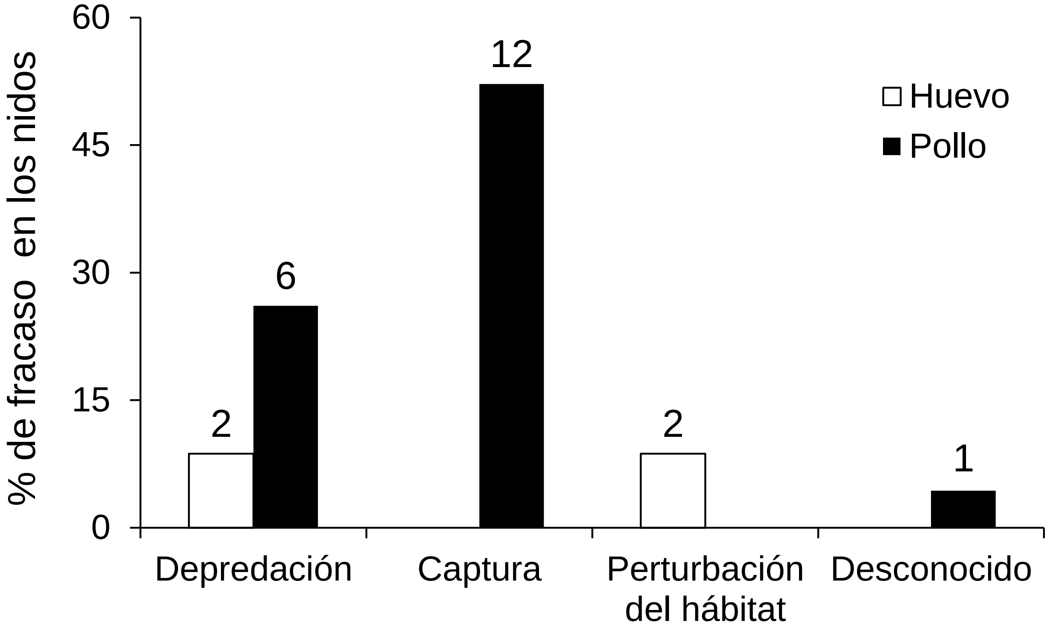


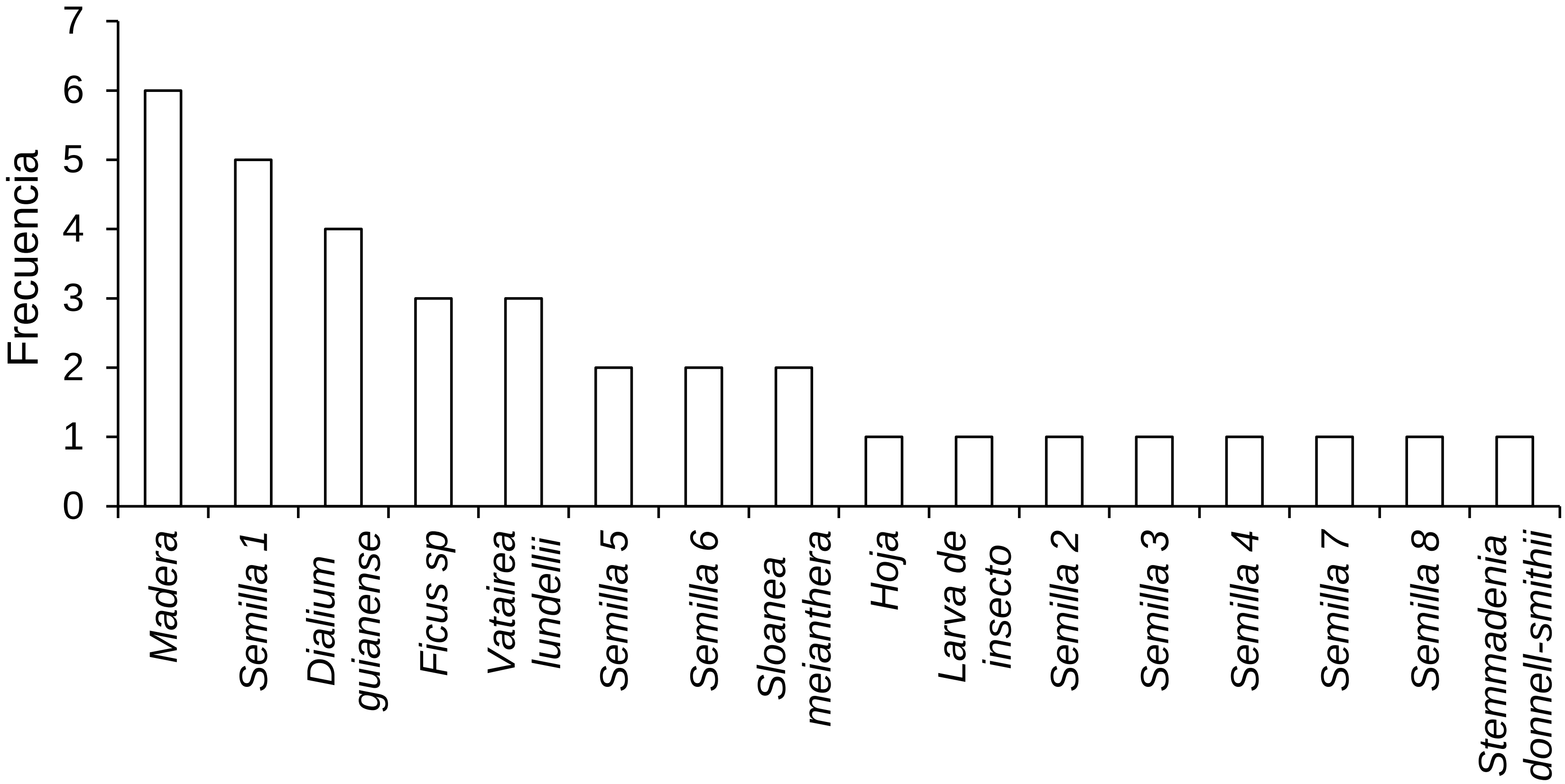
Figura 3. Causas del fracaso en los nidos del loro corona azul durante la etapa de huevo y pollo durante 2013–2016. La perturbación del hábitat ocurrió por efecto de incendios y tala del árbol-nido.



Dieta de los pollos

Se obtuvieron muestras del contenido del buche de 12 pollos en siete nidos. En las muestras se identificaron 16 componentes como alimento, incluyendo semillas de *Dialium guianense*, *Sloanea meianthera*, *Vatairea lundellii* y *Stemmadenia donnell-smithii*, así como la pulpa de *Ficus* sp., además de trozos de madera, hojas y larvas de insecto. Los elementos que tuvieron la mayor frecuencia en la dieta de los pollos fueron los trozos de madera, una semilla no identificada (semilla 1), semillas de *D. guianense*, *Ficus* sp. y *V. lundellii* (Figura 4). El componente con mayor contribución del 53.8% de la biomasa de las dieta de los pollos fue la semilla 1, seguido de semillas de *S. donnell-smithii* (15.3%), *D. guianense* (8.9%), trozos de madera (6.6%) y semillas de *V. lundellii* (4.7%).

Figura 4. Frecuencia en 12 muestras de buche de pollos del loro corona azul durante mayo 2014-2016 en Los Chimalapas, Oaxaca.



Factores que influyen en el éxito reproductivo de los loros

Se obtuvo información de supervivencia para un total de 41 nidos. El 75.6% de los nidos estuvieron ubicados en áreas perturbadas (pastizal y vegetación secundaria; *n* = 31) entre 0-40% de cobertura, mientras que solo el 24.4% de los nidos dentro del bosque primario (*n* = 10) entre 50-75% de cobertura. El número promedio de árboles dentro de la parcela de 25 m fue de 10.8 ± 70 árboles (rango = 1 – 27 árboles). La distancia promedio de los nidos al borde de la vegetación fue de 77.3 ± 77.1 m (rango = 0 – 300 m), mientras que la distancia promedio al pueblo más cercano fue de 2 ± 1.7 km (rango = 0.33 – 6.68 km).

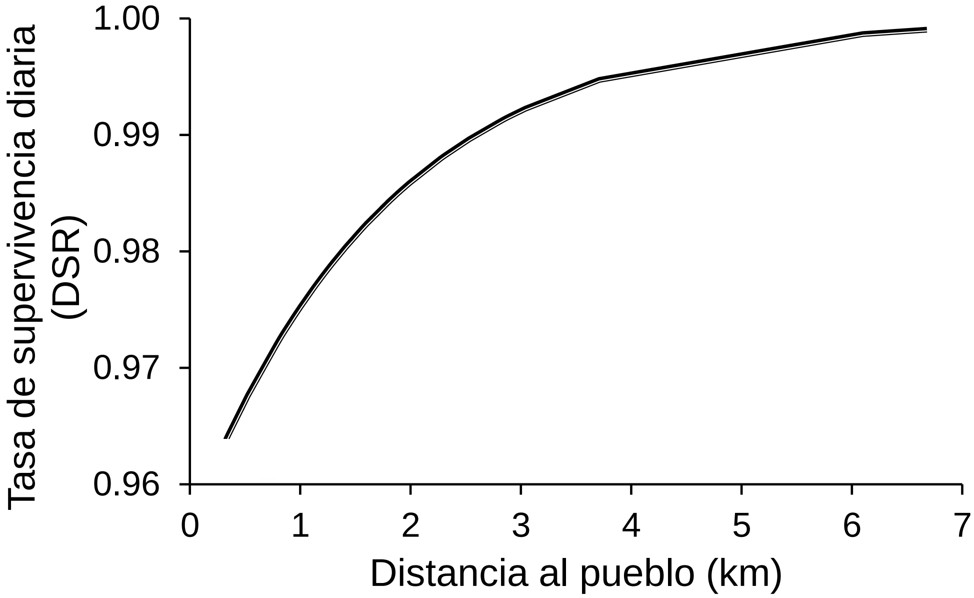
El modelo GLMM que mejor explica que un nido del loro corona azul llega a la etapa de pollo tardío, es el modelo que incorpora como factor el diámetro interno de la cavidad, y el factor a nivel paisaje de la distancia del nido al pueblo más cercano (Tabla 2). Tan solo este modelo explica una probabilidad de 0.35 de la influencia de estas dos variables sobre el éxito del nido (*wi* = 35). Por otro lado, otro modelo que podría también explicar la supervivencia del nido (Δ AICc < 2), es aquel que además incluye el factor profundidad de la cavidad con una probabilidad de 0.34. Finalmente el modelo que incluye el factor densidad de árboles podría también ser candidato, sin embargo, explica una menor probabilidad de 0.18 del efecto sobre la supervivencia del nido (Tabla 2).

Tabla 2. Relación de modelos (efectos aleatorios = ID del nido, año). Efectos fijos: AC = altura de la cavidad, PC = profundidad de la cavidad, DC = diámetro interno de la cavidad, H = hábitat (primario/alterado), C = cobertura, A = densidad de árboles, DB = distancia al borde, y DP = distancia al pueblo.

Modelos con efectos fijos	K	*N*	AICc	Δ AICc	*Wi*
S ~ DC, DP	3	41	96.4	0.00	0.35
S ~ PC, DC, DP	4	41	96.5	0.10	0.34
S ~ PC, DC, A, DP	5	41	97.7	1.30	0.18
S ~ AC, PC, DC, A, DB, DP	6	41	99.4	3.00	0.08
S ~ AC, PC, DC, A, DB, DP	7	41	101.31	5.00	0.03
S ~ AC, PC, DC, C, A, DB, DP	8	41	103.29	6.90	0.01
Nulo (S~1)	9	41	104.40	8.00	0.006
Global (S ~ AC, PC, DC, H, C, A, DB, DP)	1	41	105.29	8.90	0.004

La distancia al pueblo mostró una pendiente positiva de 2.11 ± 0.98, la cual fue significativamente diferente a cero ($Z = 2.15$, $P = 0.031$), mientras el diámetro interno del nido mostró pendiente negativa de -0.78 ± 0.41, aunque esto fue marginalmente significativo ($Z = -1.92$, $P = 0.054$). Por ello, la probabilidad de que el nido llegue a la etapa de pollo tardío incrementa significativamente cuando la distancia al pueblo es mayor. Finalmente, al considerar el efecto de la distancia al pueblo sobre la probabilidad de supervivencia de los nidos, se estimó una tasa diaria de 0.981 (IC: 0.979 – 0.983). Esto indica una tasa finita de 0.22 probabilidad de supervivencia de los nidos desde la incubación hasta la etapa de volantón (78 días; Bjork 2004). Cabe destacar que la tasa de supervivencia diaria de los nidos de los loros incrementa a 0.99 después de los 3 km de distancia del pueblo (Figura 5), por lo cual, un nido localizado ≥3 km del pueblo tendrá una mayor probabilidad finita de 0.46 de llegar a la etapa de pollo tardío.

Figura 5. Tasa de supervivencia diaria de los nidos del loro corona azul predicha por el modelo con exposición logística sobre el factor distancia al pueblo.



Relación de la abundancia de loros con la disponibilidad de recursos

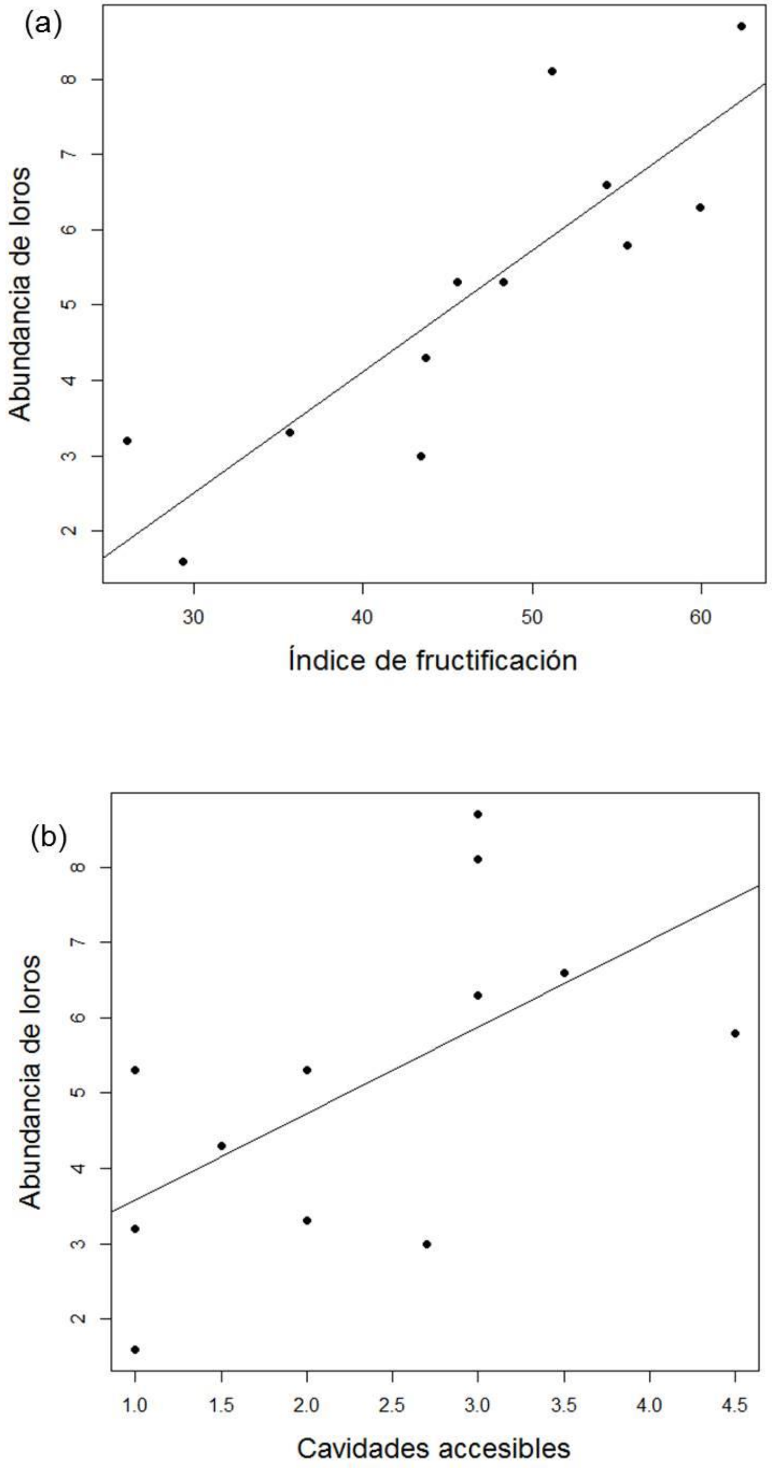
El resumen global de los datos obtenidos en los Capítulos II al IV del presente estudio, demuestran que la mayor densidad del loro corona azul se registró en los bosques conservados, donde además se obtuvo la mayor abundancia de recursos alimenticios y cavidades con condiciones adecuadas para la anidación de la especie (Tabla 3).

El modelo GLM con las variables de índice de fructificación de los árboles y densidad de cavidades adecuadas, explica en el 75% de la variación en la abundancia de los loros en cada sitio de muestreo ($D^2 = 0.75$). La abundancia del loro corona azul fue significativamente relacionada con la disponibilidad de recursos alimenticios (GLM: $D = 19.5$, $P < 0.001$) y cavidades accesibles (GLM: $D = 18.2$, $P < 0.001$), que demuestra un incremento en abundancia de loros en sitios con mayor disponibilidad de recursos alimenticios y sitios de anidación (Figura 6).

Tabla 3. Resumen global de densidad del loro corona azul y la disponibilidad de recursos alimenticios y sitios de anidación registrados por tipo de hábitat en Los Chimalapas.

Hábitat	Densidad loros / km^2	Índice fructificación	Cavidades accesibles / ha
Ribereño	35.9	52.9	2.1
Perennifolio	18.9	54.1	3.3
Secundario	3.4	32.5	1.3

Figura 6: Relación de abundancia de loros con disponibilidad de (a) recursos alimenticios y (b) sitios de anidación en cada sitio de muestreo en Los Chimalapas



Discusión

Productividad reproductiva del loro corona azul

Este estudio provee información clave sobre la ecología reproductiva del loro corona azul en el sureste de México, y proporciona los primeros datos sobre la productividad reproductiva de una población silvestre de esta especie amenazada. Durante cuatro temporadas de reproducción del loro corona azul en la región de Los Chimalapas, se determinó que el loro presenta un promedio de tamaño de puesta de 2.6 huevos por hembra, lo cual es un poco arriba de lo esperado según el tamaño de esta especie de psitácidos (Masello y Quildfeldt 2002). El loro corona azul tienen un peso de 766 gr (Forshaw 1989), y se esperaría un tamaño de puesta de 2.2 huevos (Masello y Quildfeldt 2002). Sin embargo, el loro corona azul presentó bajo éxito de eclosión del 61.7%, el cual es menor a lo encontrado para otras 11 especies de loros *Amazona*s evaluados por Rivera et al. (2014), que muestran un rango de 63 – 93% de éxito en las eclosiones. Únicamente en el caso de loro *Amazona leucocephala bahamensis* y *A. viridigenalis* se ha registrado menor porcentaje de éxito que en el loro corona azul, con 56% y 12% del éxito de eclosión respectivamente (Rivera et al. 2014).

La estimación del 5% en el éxito de anidación para el loro corona azul, es de las más bajas reportadas para los loros *Amazona*, solo en *Amazona brasiliensis* se reporta menor éxito de anidación del 0% (Rivera et al. 2014). Con relación a esto, el loro corona azul también presentó baja productividad reproductiva con tan solo el 0.5 pollos/hembra que alcanzan la etapa de pollo tardío. Incluso en 22 especies de psitácidos se reporta mayor número de 0.7 – 4.7 pollos o juveniles/pareja reproductiva que el registrado para el loro corona azul (Masello y Quildfeldt 2002). Esto incorpora a la especie entre los loros

Amazona que cuentan con la menor productividad reproductiva, particularmente de especies de loros grandes y/o amenazados como en el caso de *Amazona brasiliensis*, *A. collaria*, *A. oratrix*, y *A. ochrocephela* que presentan aún menor productividad de ≤0.3 pollos/hembra (Rivera et al. 2014).

La mayor pérdida en la productividad del loro corona azul ocurrió durante la etapa de crianza de los pollos. Factores como la disponibilidad del alimento, sitios de anidación, el éxito reproductivo en etapas anteriores, y la densidad de parejas potenciales pueden influir en la productividad del loro corona azul, sin embargo, la captura de pollos es el principal factor que origina que el 73.7% de los pollos eclosionados no lleguen a la etapa de pollo tardío. En otras especies de loros *Amazona*, la depredación natural es el principal factor de riesgo en la productividad reproductiva (Enkerlin-Hoeflich 1995, Renton y Salinas Melgoza 2004, Berkunsky 2010). Rivera et al. (2014), reportan que uno de los factores que contribuyen a que el loro *A. tucumana* muestre alta tasa de productividad y éxito reproductivo es la falta de la captura ilegal.

Factores que influyen en el éxito reproductivo

La mayoría de las características de la cavidad nido, hábitat y del paisaje poco influyen en la probabilidad de que un nido del loro corona azul llegaría a la etapa de pollo tardío. El principal factor que afecta el éxito de un nido de los loros es la distancia a los poblados humanos, donde los nidos ubicados a mayor distancia del poblado tienen mayor probabilidad de éxito. Esto se debe principalmente a la fuerte presión humana por el saqueo ilegal de los pollos de los nidos. Durante el periodo que abarcó este estudio, más del 50% de los nidos fracasaron por el saqueo de los pollos y en menor proporción por la depredación natural (28.6%). Britt et al. (2014) reportan que la captura de pollos en nidos de la guacamaya roya (*Ara macao*) es la principal causa del fracaso de los nidos en áreas no protegidas de Belice. Por su parte, Wright et al. (2001), consideran que la captura de pollos origina la mayor mortalidad de los nidos en psitácidos neotropicales. Por esta razón, la captura ilegal es una de las principales amenazas en la conservación de las especies de psitácidos neotropicales (Collar y Juniper 1992, Snyder et al. 2000). Sin embargo, esta problemática es aún mayor en áreas sin gestión de manejo (Wright et al. 2001), como es el caso de la región de Los Chimalapas.

Relación de la abundancia de loros con la disponibilidad de recursos

Nuestros resultados demuestran que el loro corona azul presenta mayor densidad en los hábitats primarios, que muestran mayor disponibilidad de recursos. Asimismo, la abundancia de los loros en los sitios de muestreo fue positivamente relacionado con la disponibilidad de recursos alimenticios y sitios accesibles de anidación. Esto cumple con uno de los componentes de la teoría de la distribución libre ideal, donde los individuos se distribuyen entre los hábitats de manera proporcional a la disponibilidad de los recursos (Fretwell y Lucas 1969). En distintas especies de psitácidos, la abundancia local del alimento y la densidad de cavidades son dos factores que influyen en su distribución, y generan cambios en la abundancia poblacional (Kinnaird et al. 2003, Marsden y Pilgrim 2003, Karubian et al. 2005, Manning et al. 2007, Rivera-Ortiz et al. 2008). Sin embargo, el presente es el primer estudio que demuestra que el loro corona azul podría seguir un modelo libre ideal entre hábitats al ser más abundante en los sitios de mayor disponibilidad de recursos alimenticios y cavidades adecuadas. Por otro lado, la dieta proporcionada por los adultos a los pollos incluyó semillas de *Dialium guianense*, *Sloanea meianthera*, *Vatairea lundellii* y frutos de *Ficus* sp., los cuales a su vez, son las especies de árboles con mayor proporción registrada en la dieta de los adultos (Capítulo III). Dichas especies de árboles son más abundantes en los bosques primarios, lo cual indica, que el loro corona azul durante la época reproductiva se distribuye hacia los hábitats conservados en busca del alimento para el desarrollo de los pollos.

Consecuencias para la adecuación

Uno de las metas de este estudio era determinar si el loro corona azul mostraría mayor éxito reproductivo en hábitats de mejor calidad al seguir un modelo de distribución libre ideal. Sin embargo, la captura de los pollos por los pobladores locales, no permitió determinar el éxito reproductivo bajo condiciones naturales, a tal grado que este factor podría indirectamente alterar la adecuación de esta especie de loro al reducir el reclutamiento de juveniles a la población, componente importante para mantener poblaciones viables. A pesar de esto, la variable profundidad de la cavidad y la variable del hábitat abundancia de árboles alrededor del nido, también puede ser un factor que podría influir en la supervivencia de los nidos.

La baja productividad reproductiva y el bajo éxito de anidación del loro corona azul en la región de Los Chimalapas, hacen que su población sea vulnerable a otras presiones antrópicas, como la degradación de los bosques y la tala selectiva de árboles maduros, que podrían reducir la disponibilidad de recursos de anidación para la especie. En México, los bosques tropicales presentan altas tasas de degradación y deforestación con una rápida conversión hacía vegetación secundaria y áreas agrícolas (de Jong et al. 2010). En la región de Los Chimalapas, tan solo durante el 2000-2003, el área ocupada por la vegetación secundaria incrementó en un 6.8% con un total de 367.2 km^2, y actualmente en esta región se estima una tasa anual de pérdida de los bosques primarios del 5.8%, principalmente por el aumento de la ganadería (Martínez-Pacheco 2012). Así pues, la captura ilegal de los pollos y la degradación de los bosques, son las dos grandes amenazas para el loro corona azul en la región de Los Chimalapas.

La falta de políticas de conservación para evitar la captura ilegal y el mejor manejo de los bosques, pondría en riesgo la permanencia a largo plazo del loro corona azul. En este sentido, estrategias de conservación, como la implementación de programas de protección de los árboles nido utilizado por el loro, y la remuneración a personas que cuenten con nidos en sus parcelas, podría aumentar el éxito reproductivo del loro corona azul. Asimismo, el correcto manejo de los bosques, y evitar la tala de árboles maduros de talla grande, que son los que reúnen las características para la formación de cavidades, permitiría la creación de cavidades potenciales para la anidación de especies amenazadas adoptadoras de cavidades.

Literatura citada

Beeton, R.J.S. 1985. The Little Corella: a seasonally adapted species. Proc. Ecol. Soc. Aust. 13:53–63.

Berkunsky, I. 2010. Ecología reproductiva del Loro Hablador (*Amazona aestiva*) en el Chaco Argentino. Ph.D. Thesis, Universidad Nacional de La Plata, La Plata, Argentina.

Bjork, R. 2004. Delineating patterns and process in tropical lowlands: Mealy Parrot migration dynamics as a guide for regional conservation planning. Ph.D. Dissertation. Oregon State University.

Britt, C.R., R. Garcia Anleu y M.J. Desmond. 2014. Nest survival of a long-lived psittacid: Scarlet Macaws (*Ara macao cyanoptera*) in the Maya Biosphere Reserve of Guatemala and Chiquibul Forest of Belize. Condor 116:265–276.

Bonebrake, T.C. y S.R. Beissinger. 2010. Predation and infanticide influences ideal free choice by a parrot occupying heterogeneous tropical habitats. Oecologia 163:385–393.

Burnham, K.P., y D.R. Anderson 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer-Verlag. New York, New York, USA.

Cody, L.M. 1985. *Habitat selection in Birds*. Academic Press, INC. San Diego California, USA.

Collar, N.J. y A.T. Juniper.1992. Dimensions and causes of the parrot conservation crisis. pp. 1–24. *En*: S.R. Beissinger y N.F.R. Snyder (eds.), *New world parrots in crisis: solutions from conservation biology*. Smithsonian Institutions Press, Washington, D.C.

de Jong, B., C. Anaya, O. Masera, M. Olguín, F. Paz, J. Etchevers, R.D. Martínez, , G. Guerrero y C. Balbontín. 2010. Greenhouse gas emissions between 1993 and 2002 from land-use change and forestry in Mexico. Forest Ecol. Manag. 260:1689–1701.

Enkerlin-Hoeflich, E.C. 1995. Comparative ecology and reproductive biology of three species of Amazona parrots in norhteastem Mexico. Ph.D. Dissertation. Texas A. and M. University.

Enkerlin-Hoeflich, E.C., J.M. Packard y J.J. González-Elizondo. 1999. Safe field techniques for nest inspections and nestling group sampling of parrots. J. Field Ornithol. 70:8–17.

Fretwell, S.D, y H.L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheor. 19:13–36.

Forshaw, J.M. 1989. *Parrots of the world*. Lansdowne Editiones, Willoughby, Australia.

Houle, A., C.A. Chapman y W.L. Vickery.2004. Tree climbing strategies for primate ecological studies. International Journal of Primatology 25:237–260.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk 118: 557–562.

Karubian, J., J. Fabara, D. Yunes, J.P. Jorgenson, D. Romo y T.B. Smith. 2005. Temporal and spatial patterns of macaw abundance in the Ecuadorian Amazon. Condor 107:617–626.

Kinnaird, M.F., T.O. O'Brien, F.R. Lambert y D. Purmiasa. 2003. Density and distribution of the endemic Seram Cockatoo *Cacatua moluccensis* in relation to land use patterns. Biol. Conserv. 109:227–235.

MacArthur, R.H., y E.R. Pianka. 1966. On optimal use of a patchy environment. Am. Nat. 100:603–609.

Manning, A.D., D.B. Lindenmayer, S.C. Barry y H.A. Nix. 2007. Largescale spatial and temporal dynamics of the vulnerable and highly mobile Superb Parrot. J Biogeogr 34:289–304.

Marsden, S. J. 1992. The distribution, abundance and habitat preferences of the salmon-crested cockatoo *Cacatua moluccensis* on Seram, Indonesia. Bird Conserv. Intn. 2:7–14.

Marsden, S. y A. Fielding. 1999. Habitat associations of parrots on the Wallacean island of Buru, Seram and Sumba. J. Biogeogr. 26:439–446.

Marsden, S.J. y K. Royle. 2015. Abundance and abundance change in the world´s parrots. Ibis. http://dx.doi.org/10.1111/ibi.12236.

Martínez-Pacheco, A.I. 2012. Monitoreo del cambio de uso de suelo en Los Chimalapas 2000-2003. pp. 86–94. *En*: Ortega del Valle D., T. Carranza López, y J. Martínez Pérez (eds.), *Una mirada desde el corazón de la jícara de oro. Experiencias de conservación en la Selva Zoque de Los Chimalapas*. WWF-México, Oaxaca, México.

Masello, J.F. y P. Quillfeld. 2002. Chick growth and breeding success of the Burrowing Parrot. Condor 104:574‑586.

R Core Team, 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (R version 3.2.3 (2015-12-10) "Wooden Christmas-Tree"). https://www.r-project.org/ (accessed 20/10/2015).

Ragusa-Netto, J. 2004. Flowers, fruits, and the abundance of the Yellow-chevroned Parakeet (*Brotogeris chiriri*) at a gallery forest in the south Pantanal (Brazil). Braz. J. Biol. 64:867–77.

Ragusa-Netto, J. 2007. Nectar, fleshy fruits and the abundance of parrots at a gallery forest in the southern Pantanal (Brazil). Stud. Neotrop. Fauna E. 42: 93–99.

Renton, K. y A. Salinas Melgoza. 2004. Climatic variability, nest predation, and reproductive output of Lilac-crowned Parrots (*Amazona finschi*) in tropical dry forest of western Mexico. Auk 121:1214–1225.

Rivera, L.N. Poloti, E.H. Bucher y A. Pidgeon. 2014. Nesting success and productivity of Tucuman Parrots (*Amazona tucumana*) in high-altitude forest of Argentina: do they differ from lowland *Amazona* parrots? Emu 114:41–49.

Rivera-Ortíz, F.A., A.M. Contreras-González, C.A. Soberanes-González, A. Valiente-Banuet y M.C. Arizmendi. 2008. Seasonal abundance and breeding chronology of the Military Macaw (*Ara militaris*) in a semi-arid region of central Mexico. Ornitol. Neotrop. 19:255–263.

Rosenzweig, M.L. 1985. Some theoretical aspects of habitat selection. pp. 517–540. *En*: Cody, M.L. (ed.), *Habitat selection in birds*. Academic Press. San Diego California, USA.

Rosenzweig, M.L. 1991. Habitat selection and population interactions: the search for mechanism. Am. Nat. 137:S5–S28.

Shaffer, T.L. 2004. A unified approach to analyzing nest success. Auk 121:526–540.

Snyder, N., P. McGowan, J. Gilardi y A. Grajal. (eds.). 2000. *Parrots: Status Survey and Conservation Action Plan 2000-2004*. IUCN, Gland, Switzerland and Cambridge.

Torres Colín, R. 2004. Tipos de Vegetación. pp. 105–117. *En*: A.J. García-Mendoza, M.J. Ordoñez y M. Briones-Salas (eds.), *Biodiversidad de Oaxaca*. Instituto de Biología, UNAM, Fondo Oaxaqueño para la Conservación de la Naturaleza, WWF-México, Oaxaca, México.

Trejo, I. 2004. Clima. pp. 67–85. *En*: A.J. García-Mendoza, M.J. Ordoñez y M. Briones-Salas (eds.), *Biodiversidad de Oaxaca*. Instituto de Biología, UNAM, Fondo Oaxaqueño para la Conservación de la Naturaleza, WWF-México, Oaxaca, México.

Wirminghaus, J.O., C.T. Downs, M.R. Perrin y C.T. Symes. 2001. Abundance and activity patterns of the Cape Parrot (*Poicephalus robustus*) in two Afromontane forests in South Africa. Afr. Zool. 36:71–77.

Wright, T.F., C.A. Toft, E. Enkerlin-Hoeflich, J. Gonzalez-Elizondo, M. Albornoz, A. Rodríguez-Ferraro, F. Rojas-Suárez, V. Sanz, A. Trujillo, S.R. Beissinger, V. Berovides, X. Gálvez, A.T. Brice, K. Joyner, J. Eberhard, J. Gilardi, S.E. Koenig, S. Stoleson, P. Martuscelli, J.M. Meyers, K. Renton, A.M. Rodríguez, A.C. Sosa-Asanza, F.J. Vilella y J.W. Wiley. 2001. Nest Poaching in Neotropical Parrots. Conservation Biology 15:710–720.

Zuur, A.F., E.N. Ieno, N.J. Walker, A.A. Saveliev, y G.M. Smith. 2009. *Mixed effects models and extensions in ecology whit R*. Springer. New York, New York, USA.

DISCUSIÓN Y CONCLUSIÓN GENERAL

Los resultados del presente estudio demostraron que la densidad de individuos del loro corona azul (*Amazona guatemalae*) no es uniforme entre los diferentes hábitats, a pesar de que la especie puede cubrir grandes áreas en sus movimientos abarcando distintos tipos de vegetación. Además, el loro demostró selección de sitios de anidación, con la mayor abundancia de sitios adecuados para su anidación en el bosque tropical perennifolio. Por otro lado, la especie mostró una estrategia de forrajeo adaptativo donde consume los recursos alimenticios de acuerdo a su disponibilidad, con la mayor abundancia de recursos alimenticios en los bosques primarios. Por último, se comprobó que el loro sigue un modelo de distribución libre ideal, pero presenta una baja productividad reproductiva y éxito de anidación debido a la captura ilegal de los pollos. Así, los resultados de este estudio son relevantes al identificar los factores de riesgo sobre el loro corona azul en bosques modificados, y contribuyen a mejorar las estrategias de conservación para la especie.

El presente estudio amplia el conocimiento de los requerimientos ecológicos del loro corona azul (*Amazona guatemalae*). En el Capítulo I de esta tesis, se demostró que durante la época reproductiva hubo mayor densidad de loros en los bosques primarios comparado con el bosque secundario. Por el contrario, la especie raramente se registró durante la época no-reproductiva, lo que sugiere que el loro realiza movimientos amplios fuera de la región de los Chimalapas, como ha sido reportado para el loro corona azul en Petén Guatemala (Bjork 2004). Asimismo, se determinó que la estructura de la vegetación, específicamente la densidad de árboles grandes y de mayor altura de la copa, influyen en la presencia y abundancia del loro. Particularmente este patrón se ha observado en especies de psitácidos de talla grande, los cuales están más asociados con los bosques primarios, que cuentan con la mayor biomasa arbórea y mejor estado de conservación (Marsden y Fielding 1999, Kinnaird et al. 2003, Evans et al. 2005, Marsden y Symes 2006, Legault et al. 2011). Además, se obtuvo que el loro corona azul seleccionó el bosque ribereño, posiblemente porque este hábitat le brinda recursos claves durante la época reproductiva y puede ser utilizado como corredor entre parches de la vegetación. Los resultados aquí obtenidos permiten mostrar que el grado de conservación de los bosques influye en la presencia y abundancia del loro. Por lo tanto, la permanencia a largo plazo del loro corona azul, en parte, depende de la conservación y manejo de los bosques perennifolio y ribereño, tanto en las áreas de reproducción como en las áreas de migración.

En el capítulo II, se registró que más de la mitad de los nidos del loro corona azul ocurrieron en árboles de *Terminalia amazonia* y *Dialium guianense*, lo que concuerda con otros estudios que han reportado principalmente el uso de 1-3 especies de árboles para anidar por otras especies de psitácidos (Saunders et al. 1982, Snyder et al. 1987, Renton y Salinas-Melgoza 1999, Monterrubio-Rico y Enkerlin-Hoeflich 2004, Monterrubio-Rico et al. 2009, Renton y Brightsmith 2009, de la Parra-Martínez et al. 2015). Además, el loro corona azul seleccionó para anidar cavidades en árboles de gran tamaño, a mayor altura desde el suelo, y con mayor profundidad y diámetro interno. En las aves que anidan en cavidades, la selección de cavidades a mayor altura es uno de los criterios que reduce el riesgo de depredación (Li y Martin 1991, Newton 1994, Cockle et al. 2008, 2015). Por lo tanto, la selección de cavidades altas y profundas por el loro corona azul podría reducir la depredación de los nidos e incrementar el éxito reproductivo, mientras que el diámetro interno estaría relacionado con el tamaño del loro y por contar con más espacio en el nido para contener la nidada. Cabe destacar que en el presente estudio determinamos una baja densidad de cavidades, con 1.6 cavidades/ha adecuadas para la anidación del loro, las cuales estaban concentradas en los bosques primarios. En cambio, hubo pocas cavidades adecuadas en el bosque secundario y en general las cavidades se encontraban en árboles de menor tamaño y a menor altura, características que no son óptimas para la anidación del loro. Debido a que el loro corona azul tiene requerimientos específicos de anidación, su persistencia a largo plazo depende de proteger las áreas de anidación y conservar los bosques primarios que brindan sitios de anidación para los loros.

En el capítulo III obtuvimos que la disponibilidad de los recursos alimenticios varía espacial y temporalmente en los Chimalapas, siendo menor durante la época no-reproductiva y en la vegetación secundaria. Una hipótesis que surge de este estudio, es que la baja abundancia del loro registrada durante la época no-reproductiva (Capítulo I) está asociado con la reducción en fructificación de los árboles durante esta temporada del año, lo cual podría sugerir migraciones de la población de loros en Los Chimalapas. En Guatemala, en la región de Petén, el loro corona azul realiza migraciones estacionales hacia la selva Lacandona en México, como respuesta a la disminución en la disponibilidad de recursos durante la época no-reproductiva (Bjork 2004). Por lo tanto, los resultados del presente estudio, junto con el de Bjork (2004), sugieren que el loro corona azul en Mesoamérica demuestra estacionalidad en sus movimientos en respuesta a los cambios en la disponibilidad y abundancia de los recursos alimenticios. Esto lleva a pensar que existen diferencias tanto ecológicas como genéticas entre las poblaciones del loro corona azul en Mesoamérica con las poblaciones de América del sur, donde están involucrados la disponibilidad de los recursos.

Además, determinamos que durante la época reproductiva el loro corona azul en Los Chimalapas mostró un nicho alimenticio amplio y consume los recursos alimenticios de acuerdo a su disponibilidad. Esta estrategia de forrajeo podría ocurrir como respuesta a la variabilidad de los recursos alimenticios, permitiendo a la especie adaptarse ante cambios en la disponibilidad del alimento. Sin embargo, en este estudio se demostró que el bosque secundario proporciona menor abundancia de recursos alimenticos para los loros. Por lo tanto, la alta conversión de bosque primario a bosque secundario (de Jong et al 2010) podría resultar en una baja disponibilidad de recursos alimenticos para los loros, teniendo implicaciones para su reproducción, dado que en bosques degradados de Australia, las cacatúas presentan menor número de eclosiones, desarrollo de los pollos y éxito reproductivo, comparado con las cacatúas que anidan en los bosques conservados (Saunders 1982, 1986, 1990). Por lo tanto, se recomienda conservar los bosques primarios para mantener la disponibilidad de recursos alimenticios durante la época reproductiva del loro corona azul.

En el capítulo IV, se presenta por primera vez información de la productividad reproductiva de una población silvestre del loro corona azul. Los resultados demostraron que el loro presenta baja productividad y éxito de anidación, con tan solo el 0.5 pollos/hembra que alcanzan la etapa de pollo tardío (>30 días de edad). Esto concentra a la especie entre los loros *Amazona* que cuentan con la menor productividad reproductiva (Rivera et al. 2014). Particularmente, la mayor pérdida en la productividad del loro ocurrió durante la etapa de pollo, y el fracaso en los nidos del loro ocurrió principalmente por la captura de los pollos. Estos resultados difieren a lo reportado para otros loros *Amazona* donde la pérdida en la productividad ocurre principalmente por la depredación natural (Enkerlin-Hoeflich 1995, Renton y Salinas Melgoza 2004, Berkunsky 2010). En los Chimalapas, la captura ilegal de los pollos por los pobladores también afectó la tasa de supervivencia diaria de los nidos, los nidos tuvieron mayor probabilidad de supervivencia si se encontraban a mayor distancia de los poblados humanos. Esto destaca la importancia de proteger áreas de bosque perennifolio primario que se encuentra alejados de asentamientos humanos, ya que otros estudios también revelan que la captura ilegal de los pollos es mucho menor en áreas protegidas (Wright et al. 2001, Britt et al. 2014). A pesar de que los Chimalapas es una de las regiones tropicales más biodiversas en Mesoamérica (Peterson et al. 2003, Navarro Sigüenza et al. 2008), los esfuerzos por declarar a la región como la primera reserva campesina del país no han sido apoyados por el gobierno mexicano (Anaya y Álvarez 1994). Por lo tanto, es necesario desarrollar estrategias de conservación que incluyan la protección de las áreas de reproducción del loro y el manejo adecuado del bosque, así como actividades alternativas a la captura de los pollos.

Un enfoque principal del presente estudio fue determinar si el loro corona azul sigue un modelo de distribución libre ideal en el uso de los recursos. Los resultados del estudio determinaron que la abundancia de los loros en los sitios de muestreo estuvo correlacionada con la disponibilidad de los recursos alimenticios y de cavidades. Asimismo, la abundancia de los loros (Capítulo I) fue proporcional con la disponibilidad de los recursos alimenticios y de cavidades en los tres tipos de bosque (Capítulos II y III). Ambos niveles del análisis apoyan la teoría de distribución libre ideal, donde en hábitats heterogéneos la abundancia de individuos en un hábitat es proporcional a la disponibilidad de los recursos. Sin embargo, no se pudo demostrar si el éxito reproductivo entre hábitats sigue un modelo libre ideal (Bonebrake y Beissinger 2010) debido a la captura de los pollos de los nidos, a tal grado que este factor podría indirectamente perjudicar la adecuación del loro corona azul.

De acuerdo a los resultados de este estudio, se considera que evaluar los requerimientos ecológicos permite identificar los recursos críticos para la supervivencia y reproducción de especies amenazadas. Al mismo tiempo, permite generar información puntual para el desarrollo de estrategias apropiadas de conservación y manejo de los bosques, al identificar el impacto potencial de las actividades antropogénicas. En la región de los Chimalapas, los bosques primarios, son hábitats claves para el loro corona azul por brindar mayor disponibilidad de recursos alimenticios y sitios de anidación durante la época reproductiva del loro, y además, la estructura de la vegetación de los bosques conservados influye en su presencia y abundancia. Se recomienda que los esfuerzos de conservación se enfoquen en revertir las tasas de degradación de la vegetación, mantener las áreas cubiertas por el bosque tropical perennifolio y proteger los bosques ribereños. De igual manera, en las áreas sujetas a aprovechamiento forestal se debe regular la tala selectiva, ya que algunas especies de árboles como *Terminalia amazonia* y *Dialium guianense* son preferentemente utilizados como nido por el loro. Programas de apoyo como el pago de servicios ambientales deben continuar en la región, además se recomienda la implementación de sistemas agroforestales y silvopastoriles de bajo impacto. Asimismo, es necesario diseñar programas de ecoturismo a nivel regional, enfocados en la observación de aves, dicha actividad generaría ingresos económicos en los pobladores locales. Igualmente, se necesita la implementación y desarrollo de programas de educación ambiental enfocados en reducir el impacto de la captura ilegal de pollos.

Conclusión

La abundancia del loro corona azul varió entre tipos de vegetación. La especie tuvo mayor densidad en el bosque ribereño y perennifolio, y mostró selección para el bosque ribereño, siendo raramente observado en el bosque secundario. Por lo tanto, se considera que el loro corona azul es especialista del bosque primario. El loro mostró requerimientos de anidación específicos, seleccionando para anidar cavidades en árboles de talla grande, a mayor altura, profundidad y diámetro interno. La dieta del loro se basó en el consumo de semillas inmaduras, y mostró un nicho alimenticio amplio sin selección del alimento. Esto último podría ocurrir por la alta variación espacial y temporal en la disponibilidad de recursos en la región, que a su vez determina las estrategias de forrajeo por el loro. Se comprobó que el loro sigue un modelo libre ideal en su distribución entre los tipos de bosque, donde su abundancia en cada tipo de bosque fue proporcional a la disponibilidad de los recursos. En su reproducción, el loro corona azul tuvo una baja productividad reproductiva y reducido éxito de anidación, debido principalmente a la captura de los pollos.

Los resultados de cada capítulo del presente estudio destacan la importancia de los bosques primarios para el loro corona azul, mientras que se considera que el bosque secundario no es un hábitat óptimo para el loro durante su reproducción. Los dos grandes factores de riesgo para la conservación del loro corona azul es la degradación de los bosques primarios y la captura ilegal de los pollos. Por lo tanto, es necesario implementar estrategias que engloben la protección de hábitats claves, y esfuerzos para prevenir la captura ilegal de los pollos.

LITERATURA CITADA

Amuno, J.B., R. Massa y C. Dranzoa. 2007. Abundance, movements and habitat use by African Grey Parrots (*Psittacus erithacus*) in Bundongo and Mabira forest reserves, Uganda. Ostrich 78:225–231.

Andrewartha, H.G. y L.C. Birch. 1954. *The distribution and abundance of animals*. Chicago Press. University of Chicago, Chicago, USA.

Arriaga, L., Espinoza, J.M., Aguilar, C., Martínez, E., Gómez, L. y Loa, E. 2000. *Regiones terrestres prioritarias de México.* Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México.

Arizmendi, M. y L. Márquez. 2000. *Áreas de importancia para la conservación de las aves en México*. CONABIO. México D.F. México.

Badyaev, A.V., T.E. Martin y W.J. Etges. 1996. Habitat sampling and habitat selection by female wild turkeys: ecological correlates and reproductive consequences. Auk 113:636–646.

Bennett, P.M. y I.P.F. Owens. 1997. Variation in extinction risk among birds: chance or evolutionary predisposition? Proceedings of the Royal Society of London Series B, 264:401–408.

Berkunsky, I. 2010. *Ecología reproductiva del Loro Hablador (Amazona aestiva) en el Chaco Argentino*. Ph.D. Thesis, Universidad Nacional de La Plata, La Plata, Argentina.

Binford, L. C. 1989. A distributional survey of the birds of the Mexican state of Oaxaca. Ornithological Monographs 43:1–418.

BirdLife International. 2016a. BirdLife Data Zone. [Online.]

URL: http//www.birdlife.org/datazone/index.html.

BirdLife International. 2016b. Species factsheet: *Amazona guatemalae*. [Online.]

URL: http://www.birdlife.org.

Bjork, R. 2004. *Delineating patterns and process in tropical lowlands: Mealy Parrot migration dynamics as a guide for regional conservation planning*. Ph.D. Oregon State University.

Bonebrake, T.C. y S.R. Beissinger. 2010. Predation and infanticide influences ideal free choice by a parrot occupying heterogeneous tropical habitats. Oecologia 163:385–393.

Brightsmith, D.J., D. McDonald, D. Matsafuji y C.A. Bailey. 2010. Nutritional content of the diets of free-living Scarlet Macaw chicks in southeastern Peru. Journal of Avian Medicine and Surgery 24:9-23.

Britt, C.R., R.G. Anleu y M.J. Desmond. 2014. Nest survival of a long-lived psittacid: Scarlet Macaws (*Ara macao cyanoptera*) in the Maya Biosphere Reserve of Guatemala and Chiquibul Forest of Belize. Condor 116:265–276.

Cantú, J.C., M.E. Sánchez-Saldaña, M. Grosselet y J. Silva-Gómez. 2007. *Tráfico ilegal de pericos en México. "Una evaluación detallada"*. Editions Teyeliz & Defenders of Wildlife. Washington, D.C.

Challenger, A. 1998. *Utilización y conservación de los ecosistemas terrestres de México, pasado, presente y futuro*. CONABIO/Instituto de Biología, UNAM, México D.F. México.

Cockle, K., A. Bodrati, M. Lammertink y K. Martin. 2015. Cavity characteristics, but not habitat, influence nest survival of cavity-nesting birds along a gradient of human impact in the subtropical Atlantic Forest. Biological Conservation 184:193–200.

Cockle, K., K. Martin y K. Wiebe. 2008. Availability of cavities for nesting birds in the Atlantic forest, Argentina. Ornitologia Neotropical 19:269–278.

Cockle, K.L., K. Martin y M.C. Drever. 2010. Supply of tree-holes limits nest density of cavity-nesting birds in primary and logged subtropical Atlantic forest. Biological Conservation 143:2851–2857.

Cockle, K., K. Martin y K. Wiebe. 2011. Selection of nest trees by cavity-nesting birds in the Neotropical Atlantic forest. Biotropica 43:228–236.

Cody, L.M. 1985. *Habitat selection in Birds*. Academic Press, INC. San Diego California, USA.

Collar, N.J. y A.T. Juniper.1992. Dimensions and causes of the parrot conservation crisis. pp. 1-24. *En* S.R. Beissinger y N.F.R. Snyder (eds.). *New world parrots in crisis: solutions from conservation biology*. Smithsonian Institutions Press, Washington, D.C.

Crowley, G.M. y S.T. Garnett. 2001. Food value and tree selection by Glossy Black-Cockatoos *Calyptorhynchus lathami*. Austral Ecology 26:116–126.

De Labra, M.A, P. Escalante, T.C. Monterrubio-Rico y R. Coates-Estrada. 2010. Hábitat, abundancia y perspectivas de conservación de psitácidos en la reserva de Los Tuxtlas, Veracruz, México. Ornitologia Neotropical 21:599–610.

De la Maza, R. y A. Ojeda. 1989. *Diagnóstico biológico e Institucional del Estado de Oaxaca, México*. Biocenosis, A.C.

de la Parra-Martínez, S.M., K. Renton, A. Salinas-Melgoza y L.G. Muñoz-Lacy. 2015. Tree-cavity availability and selection by a large-bodied secondary cavity-nester: the Military Macaw. Journal Ornithology http://dx.doi.org/10.1007/s10336-014-1150-9.

del Hoyo, J. y N.J. Collar. 2014. *Illustrated Checklist of the Birds of the World*. Lynx Edicions, Barcelona, España.

de Jong, B., C. Anaya, O. Masera, M. Olguín, F. Paz, J. Etchevers, R.D. Martínez, , G. Guerrero y C. Balbontín. 2010. Greenhouse gas emissions between 1993 and 2002 from land-use change and forestry in Mexico. Forest Ecology and Management 260:1689–1701.

de Paiva, L.V., J. Ragusa-Netto y L.F. França. 2013. Disponibilidade de alimento e abundancia de *Ortalis canicollis* durante a estação seca em matas no Pantanal Sul, Brasil. Neotropical Biology and Conservation 8:31–40.

Díaz, S., T. Kitzberger y S. Peris. 2012. Food resources and reproductive output of the Austral Parakeet (*Enicognathus ferrugineus*) in forest of northern Patagonia. Emu 112:234–243.

Domínguez-Barradas, R. y E. Ruelas-Inzunza. 1996. Avifauna de la reserva El Ocote. *En*: M.A. Vásquez Sánchez y I. March (eds), *Conservación y Desarrollo Sustentable en la Selva El Ocote, Chiapas*. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico, D.F., México.

Enkerlin-Hoeflich, E.C. 1995. *Comparative ecology and reproductive biology of three species of Amazona parrots in norhteastem Mexico*. Ph.D. Texas A. and M. University, USA.Marsden S.J. y J.D.

Evans, B.E., J. Ashley y S.J. Marsden. 2005. Abundance, habitat use, and movements of Blue-winged Macaws (*Primolius maracana*) and other parrots in and around an Atlantic forest reserve. Wilson Bulletin 117:154–164.

Fretwell, S.D, y H.L. Lucas. 1969. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. Acta Biotheoretica 19:13–36.

Forshaw, J.M. 1989. *Parrots of the world*. Lansdown Editiones, Willoughby, Australia.

Fuller, R.J. 2012. The bird and its habitat: an overview of concepts. pp 3-36. *En*: R.J. Fuller (ed.) *Birds and Habitat, Relationships in Changing Landscapes*. Cambridge University Press, UK.

Galetti, M. 1993. Diet of the Scaly-headed Parrot (*Pionus maximiliani*) in a semi-deciduous forest in southeastern Brazil. Biotropica 25:419–425.

Greene, T.C. 1998. Foraging ecology of the Red-crowned parakeet (*Cyanoramphus novaezelandiae novaezelandiae*) and Yellow-crowned parakeet (*C. auriceps auriceps*) on Little Barrier Island, Hauraki Gulf, New Zealand. New Zealand Journal of Ecology 22:161–171.

Higgings, M.L. 1979. Intensity of seed predations on *Brosimum utile* by Mealy Parrots (*Amazona farinosa*). Biotropica 11:80.

Hilden, O. 1965. Habitat selection in birds: a review. Annales Zoologici Fennici 2:3–7.

Hilty, S.L. 1980. Flowering and fruiting periodicity in a premontane rain forest in Pacific Colombia. Biotropica 12:292–306.

Howell, S.N.G. y S. Webb. 1995. *A guide to the birds of Mexico and northern Central America*. Oxford University Press, Oxford.

INEGI. 2015. Catálogo de claves de entidades federativas, municipios y localidades. http://geoweb.inegi.org.mx/mgn2k/catalogo.jsp

Jhnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Jones, J. 2001. Habitat selection studies in avian ecology: a critical review. Auk 118:557–562.

Julliard, R., J. Clavel, V. Devictor, F. Jiguet y D. Couvet. 2006. Spatial segregation of specialists and generalists in bird communities. Ecology Letters 9:1237–1244.

Kinnaird, M.F, T.G. O'Brien y S. Suryadi. 1996. Population fluctuation in Sulawesi Red-knobbed Hornbills: tracking figs in space and time. Auk 113:431–440.

Legault, A., V. Chartendraul, J. Theuerkauf, S. Rouys y N. Barré. 2011. Large-scale habitat selection by parrots in New Caledonia. Journal Ornithology 152:409–419.

Levey, D.J. 1988. Spatial and temporal variation in Costa Rican fruit and fruit-eating bird abundance. Ecological Monographs 58:251–269.

Li, P. y T.E. Martin. 1991. Nest-site selection and nesting success of cavity-nesting birds in high elevation forest drainages. Auk 108:405–418.

Lira-Torres, I. y M. Briones-Salas, F.R. Gómez de Anda, D. Ojeda-Ramírez y A. Peláez Acero. 2014. Uso y aprovechamiento de la fauna silvestre en la selva Zoque, México. Acta Zoológica Mexicana 30:74–90.

Loyd, H. 2004. Habitat and populations estimates of some threatened lowland forest bird species in Tambopata, south-east Peru. Bird Conservation International 14:261–277.

Loiselle, B.A. y J.G. Blake. 1991. Temporal variation in birds and fruits along an elevational gradient in Costa Rica. Ecology 72:180–193.

MacArthur, R.H., y E.R. Pianka. 1966. On optimal use of a patchy environment. American Naturalist 100:603–609.

Manly, B.F.J., L.L. McDonald, L.D. Thomas, T.L. McDonald y W.P. Erickson. 2002. *Resource section by animals: statistical design and analysis for field studies.* Chapman and Hall, London.

Marsden, S. y A. Fielding. 1999. Habitat associations of parrots on the Wallacean island of Buru, Seram and Sumba. Journal of Biogeography 26:439–446.

Marsden, S.J. y C.T. Symes. 2006. Abundance and habitat associations of parrots at a hillforest site in Papaua New Guinea. Pacific Conservation Biology 12:15–21.

Martínez-Pacheco, A.I. 2012. Monitoreo del cambio de uso de suelo en Los Chimalapas 2000-2003. Pp. 86-94. *En*: Ortega del Valle D., T. Carranza López, y J. Martínez Pérez (eds.). *Una mirada desde el corazón de la jícara de oro. Experiencias de conservación en la Selva Zoque de Los Chimalapas*. WWF-México, Oaxaca, México.

Masera, O.R, M.J. Ordóñez y R. Dirzo. 1997. Carbon emissions from Mexican forests: current situation and long-term scenarios. Climatic change 35:265–295.

Matuzak, G.D., M.B. Bezy y D.J. Brightsmith. 2008. Foraging ecology of parrots in a modified landscape: seasonal trends and introduced species. Wilson Journal Ornithology 120:353–365.

Monterrubio-Rico T.C. y E. Enkerlin-Hoeflich. 2004. Present use and characteristics of Thick-billed Parrot nest sites in Northwestern Mexico. Journal of Field Ornithology 75:96–103.

Monterrubio-Rico, T.C., J.F. Charre-Medellín, C. Pacheco-Figueroa, S. Arriaga-Weiss, J.D. Valdez-Leal, R. Cancino-Murillo, G. Escalona-Segura, C. Bonilla-Ruiz y Y. Rubio-Rocha. 2016. Distribución potencial histórica y contemporánea de la familia Psittacidae en México. Revista Mexicana de Biodiversidad 87:1103–1117.

Monterrubio-Rico T.C., J. Ortega-Rodríguez, M.C. Marín-Togo, A. Salinas-Melgoza y K. Renton. 2009. Nesting habitat of the Lilac-crowned Parrot in a modified landscape in Mexico. Biotropica 41:361–368.

Morales-Pérez, L. 2005. *Evaluación de la abundancia poblacional y recursos alimenticios para tres géneros de psitácidos en hábitats conservados y perturbados en la costa de Jalisco, México*. Tesis de Maestría. Instituto de Biología. UNAM. México, D.F.

Navarro Sigüenza, A.G., L.C. Márquez y H.O. Monroy. 2008. Vertebrados terrestres de Los Chimalapas: una prioridad de conservación. CONABIO. Biodiversitas 77:10–15.

Newton, I. 1998. *Population limitation in birds*. Academic Press. London.

Newton I. 1994. The role of nest sites in limiting the numbers of hole-nesting birds: a review. Biological Conservation 70:265–76.

Ortiz-Maciel, S.G., C. Hori-Ochoa y E. Enkerlin-Hoeflich. 2010. Maroon-fronted Parrot (*Rhynchopsitta terrisi*) breeding home range and habitat selection in the northern Sierra Madre Oriental, Mexico. Wilson Journal Ornithology 122:513–517.

Partridge, L. 1978. Habitat selection. pp351–376. *En*: Krebs, J.R. y N.B. Davies (eds.) *Behavioural Ecology: and evolutionary approach*. Blackwell Scientific Publication.Oxford.

Peterson, A.T., A.G. Navarro-Sigüenza, B.E. Hernández-Baños, G. Escalona-Segura, F. Rebon-Gallardo, E. Rodríguez-Ayala, E.M. Figueroa-Esquivel y L. Cabrera-García. 2003. The Chimalapas Region, Oaxaca, Mexico: a high-priority region for bird conservation in Mesoamerica. Bird Conservation International 13:227–253.

Renton, K. 2001. Lilac-crowned Parrots diet and food resource availability: resource tracking by a parrot seed predator. Condor 103:62–69.

Renton, K. 2006. Diet of adult and nestling Scarlet macaw in Southwest Belize, Central America. Biotropica 38:280–283.

Renton, K. y A. Salinas-Melgoza. 2004. Climactic variability, nest predation, and reproductive output of Lilac-crowned Parrots (*Amazona finschi*) in tropical dry forest of western Mexico. Auk 121:1214–1225.

Renton, K. y A. Salinas-Melgoza. 1999. Nesting behavior of the Lilac-crowned Parrot. Wilson Bulletin 111:488–493.

Renton, K., A. Salinas-Melgoza, M.A. De Labra-Hernández y S.M. de la Parra-Martínez. 2015. Resource requirements of parrots: nest site selectivity and dietary plasticity of Psittaciformes. Journal of Ornithology http://dx.doi.org/10.1007/s10336-015-1255-9.

Renton, K. y D. Brightsmith. 2009. Cavity use and reproductive success of nesting macaws in lowland forest of southeast Peru. Journal of Field Ornithology 80:1–8.

Rivera, L.N. Poloti, E.H. Bucher y A. Pidgeon. 2014. Nesting success and productivity of Tucuman Parrots (*Amazona tucumana*) in high-altitude forest of Argentina: do they differ from lowland *Amazona* parrots? Emu 114:41–49.

Rotenberry, J.T. y J.A. Wiens. 1980. Habitat structure, patchiness, and avian community in north American steppe vegetation: a multivariate analysis. Ecology 61:1228–1250.

Rzedowski, J. 1978. *Vegetación de México*. Editorial Limusa. México.

Salas-Morales, S.H., L. Schibli y E. Torres-Bahena. 2001. La importancia ecológica y biológica. pp 29-41. *En*: Aparicio Cid, R. (ed.) *Chimalapas. La última oportunidad*. World Wildlife Found Programa México y Secretaría de Medio Ambiente, Recursos Naturales y Pesca. México D.F. México.

Salinas-Melgoza, A. y T.F. Wright. 2013. Behavioral plasticity of the threatened parrot in human-modified landscape. Biological Conservation 159:303–312.

Saunders, D.A. 1986. Breeding season, nesting success and nestling growth in Carnaby’s Cockatoo, *Calyptorhynchus funereus latirostris*, over 16 years at Coomallo Creek, and a method for assessing the viability of population in other areas. Australian Wildlife Research 13:261–73.

Saunders, D.A. 1990. Problems of survival in an extensively cultivated landscape: the case of the Carnaby´s Cockatoo *Calyptorhynchus funereus latrirostris*.Biological Conservation 54:277–290.

Saunders, D.A., G.T Smith y I. Rowley. 1982. The availability and dimensions of tree hollows that provide nest sites for cockatoos (Psittaciformes) in Western Australia. Australian Wildlife Research 9:541–556.

Stahala, C. 2008. Seasonal movements of the Bahama Parrot (*Amazona Leucocephala bahamensis*) between pine and hardwood forests: implications for habitat conservation. Ornitologia Neotropical 19:1–8.

SEMARNAT 2010. Norma Oficial Mexicana NOM-059-ECOL-2010. Protección ambiental-Especies nativas de México de flora y fauna silvestres-Categorías de riesgo y especificaciones para su inclusión, exclusión o cambio-Lista de especies en riesgo. Secretaria de Medio Ambiente y Recursos Naturales, México, D.F., México.

Simão, I., F.A. Maës dos Santos y M.A. Pizo. 1997. Vertical stratification and diet of psittacids in a tropical lowland forest of Brazil. Ararajuba 5:169–174.

Shodi, N.S., M.R.C. Posa, T.M. Lee y I.G. Warkentin. 2008. Effects of disturbance or loss of tropical rainforest on birds. Auk 125:511–519.

Snyder, N.F.R., J.W. Wiley y C.B. Kepler. 1987. *The parrots of Luquillo: natural history and conservation of the Puerto Rican Parrot*. Western Foundation of Vertebrate Zoology, Los Angeles, California. USA.

Snyder, N., P. McGowan, J. Gilardi, y A. Grajal. 2000. *Parrots. Status survey and conservation action plan 2000-2004*. IUCN, Gland, Switzerland and Cambridge, UK.

Stahala, C. 2008. Seasonal movements of the Bahama Parrot (*Amazona Leucocephala bahamensis*) between pine and hardwood forests: implications for habitat conservation. Ornitologia Neotropical 19:1–8.

Stojanovic, D., M. Webb, D. Roshier, D. Saunders y R. Heinsohn. 2012. Ground-based survey methods both overestimate and underestimate the abundance of suitable tree-cavities for the endangered Swift Parrot. Emu 112:350–356.

Tilman, D. 1982. *Resource competition and community structure*. Princenton University Press, Princeton, New Jersey.

Trejo, I. 2004. Clima. pp 67–85. *En* García-Mendoza, A.J., M.J. Ordoñez y M. Briones-Salas (eds.) *Biodiversidad de Oaxaca*. Instituto de Biología, UNAM, Fondo Oaxaqueño para la Conservación de la Naturaleza, WWF-México, México.

Torres Colín, R. 2004. Tipos de Vegetación. pp. 105-117. *En:* García-Mendoza, A.J., M.J. Ordoñez y M. Briones-Salas (Eds.). Biodiversidad de Oaxaca. Instituto de Biología, UNAM, Fondo Oaxaqueño para la Conservación de la Naturaleza, WWF-México, México.

Wendt, T. 1987. Las selvas de Uxpanapa, Veracruz-Oaxaca, México: Evidencia de refugios florísticos cenozoicos. Anales del Instituto de Biología UNAM 58:29–54.

Wenner, T.J., M.A. Russello, y T.F. Wright. 2012. Cryptic species in a Neotropical parrot: genetic variation within the *Amazona farinosa* species complex and its conservation implications. Conservation Genetics 13:1427–1432.

Wiens, J.A. 1989. *The ecology of bird communities*. Vol 1. Foundations and patterns. Cambridge University Press. Cambridge.

Wiens, J.A. 1984. Resource systems, populations, and communities. pp 397–436. *En*: Price, P.W., C.N. Slobodchikoff y S.G. Williams (eds.) *A new ecology: novel approaches to interactive systems*. Wiley-Interscience, New York, New York, USA.

Whitney, K.D. y T.B. Smith. 1998. Habitat use and resource tracking by African *Ceratogymna* hornbills: implications for seed dispersal and forest conservation. Animal Conservation 1:107–117.

Wright, T.F., C.A. Toft, E. Enkerlin-Hoeflich, J. Gonzalez-Elizondo, M. Albornoz, A. Rodríguez-Ferraro, F. Rojas-Suárez, V. Sanz, A. Trujillo, S.R. Beissinger, V. Berovides, X. Gálvez, A.T. Brice, K. Joyner, J. Eberhard, J. Gilardi, S.E. Koenig, S.

Stoleson, P. Martuscelli, J.M. Meyers, K. Renton, A.M. Rodríguez, A.C. Sosa-Asanza, F.J. Vilella y J.W. Wiley. 2001. Nest Poaching in Neotropical Parrots. Conservation Biology 15:710–720.