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Ecology of rare and abundant raptors on an oceanic island: the Sharp-shinned Hawk and Red-tailed Hawk in Puerto Rico

By

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Ecology of rare and abundant raptors on an oceanic island: the Sharp-shinned Hawk and Red-tailed Hawk in Puerto Rico

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Reliable estimates of species abundance, distribution, and population trajectories are critical in conservation and management. However, for many tropical species that information is missing. We conducted Sharp-shinned Hawk (SSHA) searches during the breeding seasons of 2013, 2014, and 2016 in eight montane forest reserves and their adjacent private lands of Puerto Rico. Further, we developed a maximum entropy model (MaxEnt) of the SSHA's potential distribution using the following environmental variables: aspect, canopy closure, elevation, rainfall, slope, and terrain roughness. Elevation accounted for 89.8% of model fit, predicting the greatest probability of occurrence (>60%) at elevations above 900 m. The model estimated 0.6%Puerto Rico (56.1 km^2) has the greatest probability of occurrence. We developed a periodic population matrix model to describe influence of early life stages on population growth of the Red-tailed Hawk (RTHA) in eastern Puerto Rico. Our results suggest that the RTHA population has an average annual population increase of 5%, with rates differing between highlands ($\lambda_h = 1.05$) and 27% lowlands ($\lambda_l = 1.27$). Adult survival was the most important population growth parameter, with more effect in highlands (elasticity = 0.86) than in lowlands (elasticity= 0.53). Sensitivity of λ to changes in nestling survival was greater than for other life-stages (sensitivity lowlands = 0.46, sensitivity highlands = 0.48). I developed an open population N-mixture model to estimate abundance, availability, and detection probability of RTHA in the Luquillo Mountains and western Cordillera Central. The abundance estimates were 0.05 RTHA/ha, with an availability of (ϕ) = ~1 RTHA/per survey point and a detection probability (r) = ~0.25. In Luquillo Mountains, abundance was positively influenced by slope and elevation. In the western Cordillera Central, abundance of RTHA was constant across elevation, slope, and canopy closure. Detection probability decreased with increasing slope and wind conditions and showed a gradual small negative decrease with slope with reduced winds conditions. My findings are a contribution to our knowledge to how population traits and ecological constraints imposed by insular environments are influencing distribution, abundance, and population dynamics of raptors to propose management or conservation schemes.

DEDICATION

With immense love and gratitude to the most important women in my life, Beatriz and Gail. Thanks for your patience, love, encouragement, and unconditional support along this journey, this is for you.

In loving memory of my father Agustin, we did it Dad!!

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CHAPTER I

GENERAL INTRODUCTION

Despite occupying a small fraction of the Earth's surface (~7%), islands are recognized as an important repository of global biodiversity (Myers et al. 2000, Kreft et al. 2008, Donald et al. 2013). Geographical and ecological isolation make island biodiversity rich in endemism and make island environments highly vulnerable to perturbation, rendering them particularly important for global biodiversity conservation (Blackburn et al. 2004, Donald et al. 2013). Insular populations have developed common characteristics as a result of adaptations to island environments such as reduced aggression, reduced dispersion, greater adult and juvenile survival rates, low productivity, and long breeding periods, which together result in smaller home ranges with great overlap, high densities, and populations characterized by adult individuals (Gliwicz 1980, Adler and Levins 1994).

Many adaptations exhibited by island biotas have provided some of the best models to understand the evolutionary mechanisms responsible for speciation processes (Grant 2001, Donald et al. 2013, Aleixandre et al. 2013). However, how island population traits are driving species abundances and distributions is still poorly understood, limiting our capability to develop management and conservation measures. The vulnerability of island environments and island populations is characterized by high rates of species extinctions—around 90% of known extinct species and subspecies of birds in the last five centuries have been island endemics (Donald et al. 2013).

Organisms in oceanic islands may exhibit unique resource use patterns, including niche expansion or shifts, because of release from interspecific competition (Abbott 1980, Baker-Gabb 1986, Newton 2003, Grant and Grant 2006). For some island species, this release may result in greater abundance and a wider range of habitats used compared to mainland counterparts, a phenomenon described as density compensation (Crowell 1962, MacArthur et al. 1972, Blondel 2000). Habitat heterogeneity can greatly influence species abundance and distribution where abundance is likely to be higher in habitats most strongly selected by individuals (Brown 1984, Brown 1995, Boyce et al. 2016). However, individuals may select sites that provide all their life history requirements but be forces to populate other locations as abundance and density increase (Fretwell and Lucas 1970, Krüger 2002, Boyce et al. 2016).Along with density-dependent factors (i.e., intraspecific and interspecific competition, predation, and parasitism), temporal variation and spatial arrangement of habitats can also affect the overall population abundance and distribution of individuals (Dunning et al. 1992, Cody 1985, Morris 2006, Jonzén 2008, Krüger et al. 2012). While island populations can occupy a wide range of habitat and environmental conditions, local abundance is affected by species' niche and population dynamics (Brown 1984, Brown 1995, Pulliam 2000, Harte 2011).

Together, population dynamics and niche space can be reliable predictors of local abundance and overall distribution of species (Brown 1984, Brown 1995, Pulliam 2000, Harte 2011). Widely distributed species are usually generalists, exhibiting broad ecological niches that allow them to persist in a wide range of habitats. Conversely, species with narrow niches (i.e., specialists) are usually restricted to areas harboring narrow ecological requirements (Brown 1984, Kunin and Gaston 1997). Generalist forms of a foraging specialist may occur under tropical island conditions such as low seasonality, high density, low territoriality, low inter-specific competition, and high food availability and predictability (Van Valen 1965, Roughgarden 1979, Glasser 1982, Werner and Sherry 1987). However, certain island traits may limit species' distributions, habitats, or resources used based on their intrinsic characteristics. For example, habitat and ecological specialization may occur in species with reduced dispersion, small ranges, and low populations living in a fragmented landscape species because of adaptation to local conditions (Kickpatrick and Barton 1997, Newton 1998, Krüger and Radford 2008).

The Red-tailed Hawk (*Buteo jamaicensis*) and Sharp-shinned Hawk (*Accipiter striatus*) are two raptors with resident populations in North America, Central America and the Greater Antilles (Bildstein and Meyer 2000, Ferguson-Lees and Christie 2001, Preston and Beane 1993). The Red-tailed Hawk is a widespread and common raptor in North America and it inhabits a wide variety of open and semi open habitats (Preston and Beane 1993). In North America, the Sharp-shinned Hawk is similarly widespread, nesting in large stands of different forest associations (Bildstein and Meyer 2000). Both species have been well studied in North America, but knowledge of their ecology in Neotropical environments, including insular forms is limited (Delannoy 1997, Santana and Temple 1988, Bildstein and Meyer 2000, Nimitz 2005, Preston and Beane 1993). The Caribbean subspecies of the Red-tailed Hawk (*B. j. jamaicensis*; hereafter, RTHA) and the endemic subspecies of Sharp-shinned Hawk Rico (*A. s. venator*; hereafter, SSHA)are permanent residents in Puerto and both species exhibit island traits such as smaller clutches, less productivity, and greater densities (Delannoy 1984, Santana and Temple 1988, Nimitz 2005, Llerandi 2006).

The RTHA is the most common diurnal raptor in Puerto Rico (Rivera-Milán 1995, Nimitz 2005, Vilella and Nimitz 2012). The species exhibits extensive home range overlap and a greater population abundance than mainland conspecifics, reaching its greatest concentrations in the eastern portion of the island (Raffaele 1992, Santana and Temple 1988, Rivera-Milán 1995, Boal et al. 2003, Nimitz 2005, Llerandi 2006). Moreover, contrary to continental populations that nest in open areas, RTHAs in Puerto Rico occur in all life zones of the island and nest across all elevations, including closed-canopy montane forest (Santana and Temple 1988, Boal et al. 2003, Nimitz 2005, Llerandi 2006). In mature forests of Puerto Rico, the RTHA is associated with openings and roadside habitats and favors landscapes characterized by greater patch and edge density (Santana et al. 1986, Santana and Temple 1988, Nimitz 2005, Vilella and Nimitz 2012). The RTHA is the most important native predator of the critically endangered Puerto Rican Parrot (*Amazona vittata*), accounting for most of the parrot mortalities in El Yunque National Forest (Snyder et al. 1987, White et al. 2005, Llerandi 2006).

Contrary to the RTHA, the Caribbean SSHA subspecies appears to be declining (Delannoy 1997). Except for the SSHAsin Puerto Rico, information for the other insular subspecies is virtually absent (Bildstein and Meyer 2000). The Puerto Rican SSHA is an endangered woodland raptor with small populations known from montane forest reserves on the island (Delannoy 1997, USFWS 1997). Island-wide estimates recorded in five forest reserves encompassing 285.6 km^2 indicated the SSHA population declined from 240 individuals in 1985 to approximately 82 individuals by the late 1990s (Delannoy

1997). This observed decline may be a result habitat loss, forest fragmentation, high rate of nestling mortality by botfly parasitism (*Philornis spp.*), and possible impact of recent hurricanes (Wiley 1986, Delannoy and Cruz 1988, Boose et al. 2004, Flynn et al. 2010).Information on SSHA population status and presence is lacking for private lands in Puerto Rico, particularly the Cordillera Central.

Insular raptors play a key role as top predators in islands as mammals are absent. Understanding the factors that are driving their abundance and the distribution of top predators is essential to design and implement conservation of land management measures for endangered tropical islands species. In this study, I predicted abundance and distribution of a top-level generalist predator, the RTHA, as a function of local environmental landscape conditions (i.e., wind speed, mean slope, elevation, and canopy closure). In addition, I assessed habitat characteristics that might influence population parameters and restrict-distribution of island specialist such as the SSHA (Brown 1984, Binckley and Resetarits 2005, Mayor et al. 2008). My study addressed ecological aspects determining the distribution of two sympatric tropical island raptors (RTHA and SSHA), species-habitat relationships, and population dynamics. Specifically, this study was designed to provide new knowledge for conservation and management of native predators in an oceanic tropical island. The objectives of my study were to:

1. Estimate RTHA populations in the Luquillo Mountains and Cordillera Central,
2. Develop a population sensitivity model to determine influence of critical life stages on RTHA population growth,
3. Develop landscape habitat models to identify variables contributing to RTHA abundance in Luquillo Mountains and Cordillera Central,

4. Develop a spatial distribution model for SSHA in Puerto Rico, and,
5. Provide conservation and management recommendations for RTHA and SSHA in Puerto Rico.

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CHAPTER II

STUDY AREA

Puerto Rico and its satellite islands (17°45’ 18°30’ N and 65°45’, 67°15’W) are the smallest and easternmost islands of the Greater Antilles. The territorial extent of Puerto Rico consists of the main island and the satellite islands of Culebra and Vieques to the east; Desecheo, Mona, and Monito to the west; and numerous other small islands and cays. The main island of Puerto Rico is 178 km long and 58 km wide, comprising an area of 8,740 km^2 (Daly et al. 2003). The landscape is predominately mountainous; dominant physiographic formations include the central mountain range (i.e., Cordillera Central) running east-west, the moist karst forest extending across the island’s northern region, the Cayey Mountains in the south-central region, and the Luquillo Mountains on the island’s northeastern side (Figure 1.1). Mountains and hills comprise 75% of Puerto Rico (Gould et al. 2008).

Puerto Rico’s topography imparts a strong influence on weather, with decreasing precipitation from the windward, northern side of the island to the leeward rain shadow on the southwest. Two annual rainfall peaks occur, one between April and May and another from October to December. Mean annual rainfall ranges from below 90 cm in the subtropical dry life zone to over 400 cm in the wet rainforest (Daly et al. 2003, Gould et al. 2008). Average annual temperatures range from 22 ºC to 25 ºC (Daly et al. 2003).

While a relatively small island, Puerto Rico encompasses six bioclimatic life zones. These include subtropical dry forest, lowland moist forest, subtropical wet forest, lower montane wet forest, subtropical rain forest, and lower montane rain forest zones (Ewel and Whitmore 1973). Except for the subtropical dry forest, all other life zones on the island were included in my study sites. More than one-half of the island is lowland moist forest, located from 0 to 400 m, average annual precipitation of 100 to 220 cm, and dominated by semi-deciduous forest associations with a canopy averaging 8 m. Subtropical wet forest occurs at middle elevations, ranging from 400 to 700 m, with an average annual rainfall of 200 to 400 cm, and is characterized by evergreen forests with a continuous canopy of about 20 m. The subtropical lower montane wet forest occurs between 700 and 1,000 m and annual rainfall averages 225 cm with forests dominated by evergreen species characterized by an open crown.

Localized on the northeastern side of the island, the Luquillo Mountains region has the most complex physiographic features (Ewel and Whitmore 1973). Subtropical lower rain forest covers the smallest area in Puerto Rico and is restricted to the windward region of the Luquillo Mountains along an altitudinal belt just above the subtropical rain forest and below the subtropical lower montane wet forest. The structure of the subtropical lower rain forest is similar to the subtropical lower montane wet forest, but with a mean annual rainfall up to 400 cm and a relative humidity of 98%. The subtropical rain forest of the Luquillo Mountains represents the wettest region of Puerto Rico, with mean annual rainfall of 380–400 cm. The structure and taxonomic composition of this forest is similar to the subtropical wet forest but without water limitation (Ewel and

Whitmore 1973). The landscape of the Luquillo Mountains reflects past disturbance from agricultural activities and is characterized by four dominant forest types: tabonuco (*Dacryodes excelsa*), palo colorado (*Cyrilla racemiflora*), sierra palm (*Prestoea montana*), and elfin woods forest, which dominates ridge tops and peaks (Scatena 1989).

The Cordillera Central is the principal mountain range of Puerto Rico, extending across the midsection of the island. The Cordillera Central encompasses four of six life zones. Annual precipitation ranges from 200 to 400 cm (Ewel and Whitmore 1973) and elevation ranges from 550 to 1130 m. The landscape is dominated by secondary forest, active and abandoned coffee plantations (*Coffea* spp.), and urban areas. However, significant areas of mature secondary forest (i.e., ≥ 60 years old) remain characterized by *Dacryodes excels*, *Sloanea berteriana*, and *Manilkara bidentata* (Ewel and Whitmore 1973, Marcano-Vega et al.2002). The lower montane forests of the Cordillera Central support three different vegetation associations tightly related to topography (Ricart and Padrón 2010). Those associations include: (1) windy cliff vegetation over shallow soil and steep slopes, regularly exposed to strong winds; common species include *Clusia rosea*, *Tabebuia heamanha*, and *Guettarga pungenus*; (2) Neotropical hardwood mixed forest, characterized by deep soils and smooth slopes, including species such as *Mataiga domingensis*, *Prestoea montana*, and *Solaena amygdalia*; and (3) lowland-palm forest, similar to the *Podocarpus* association but occurring in deeper soils and dominated by sierra palm (*Prestoea montana*).

Puerto Rico is characterized by a diverse, dynamic, fragmented, and highly heterogeneous landscape with 70 separate land cover units described in the Puerto Rico

GAP Analysis (Gould et al. 2008). According to the Puerto Rico GAP Analysis, 53% of the island is covered by woody vegetation encompassing 49 land cover units. Of this, 40% of the woody vegetation is classified as forest (> 60% of tree cover). Most forest vegetation is represented by low-and mid-elevation moist woody vegetation cover (27%), followed by upper-elevation wet woody vegetation (18%) and dry woody vegetation (8%). Other vegetation cover types include coastal forest (mangroves and *Pterocarpus* swamp forest), representing 1% of the island's surface, and coffee plantations, at around 6% (Helmer et al. 2002, Gould et al. 2008). Grasslands are the second most abundant land cover formation (32%), largely the result of human activity (i.e., agriculture) and natural perturbations (Helmer et al. 2002, Gould et al. 2008). Brackish and fresh water seasonally flooded wetlands represent 4% of the total surface and are dominated by herbaceous vegetation (Gould 2008). Around 11% of the island surface includes urbanized areas. While these are present at all elevations, urban development is concentrated in the coastal plains and lower elevation hills (Martinuzzi et al. 2007).

Following the Spanish colonization of Puerto Rico, European settlers gradually removed most of the coastal and low elevation forest (Birdsey and Weaver 1982). By the end of the nineteenth century, pastures dominated the island landscape, representing over 50% of the total island surface (Wadsworth 1950). This deforestation continued into the twentieth century and by the 1940s, forests represented only 6% of Puerto Rico's vegetation cover. Fragments of remaining forest persisted mainly at higher elevations, thanks in part to coffee agriculture (Koenig 1953, Birdsey and Weaver 1982, Thomlinson et al, 1996, Franco et al. 1997). During the second half of the twentieth century the economy shifted from agriculture to manufacturing, leading to abandonment of agricultural lands and resulting in expansion of secondary forests (Dietz 1986, López et al. 2001, Marcano-Vega et al. 2002). Timber plantations and traditional shade coffee agricultural practices played an important role in the reforestation of Puerto Rico (Birdsey and Weaver 1982). Tree plantations were common in private and public lands in Sierra de Luquillo and Cordillera Central, where the most common species were Caribbean pine (*Pinus caribaea*), eucalyptus (*Eucalyptus robusta*), teak (*Tectona grandis*), and the maria tree (*Calophyllum brasiliense*) (Birdsey and Weaver 1982, Ricart and Padrón 2010).

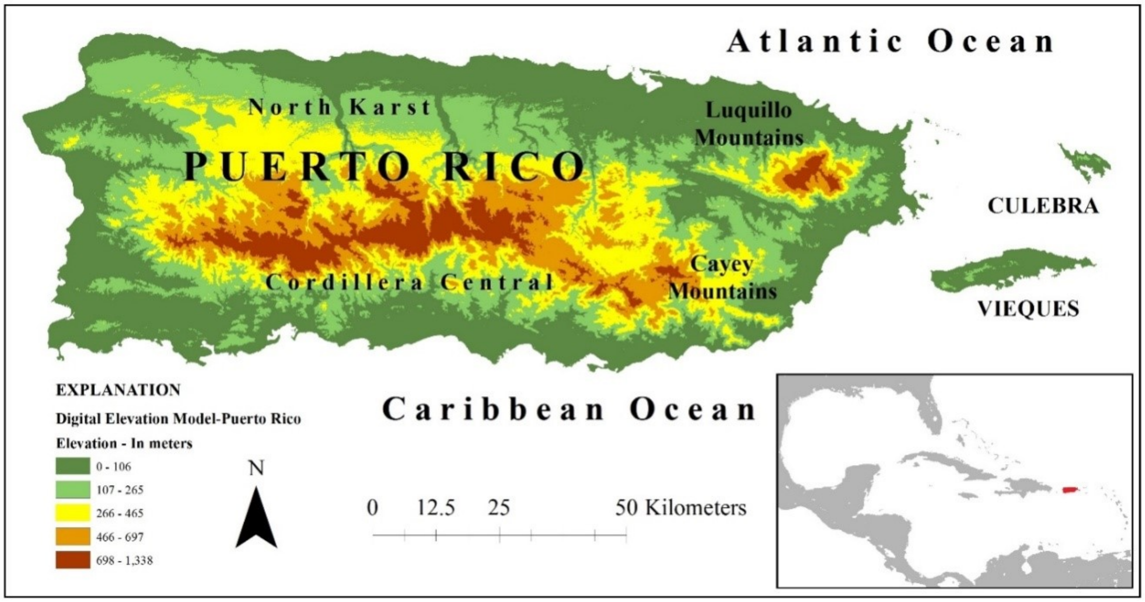

Figure 2.1 Map of Puerto Rico and its main satellite islands indicating major physiographic formations and location in the Caribbean archipelago (inset).

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CHAPTER III

CONSERVATION STATUS ASSESSMENT OF THE SHARP-SHINNED HAWK, AN ENDANGERED INSULAR RAPTOR IN PUERTO RICO

This chapter was previously published (Gallardo and Vilella 2017). Reprinted by Permission by John Wiley and Sons Press (Appendix A).

Abstract

Sharp-shinned Hawks (*Accipiter striatus*) are forest raptors that are widely distributed in the Americas. A subspecies endemic to Puerto Rico (*A. s. venator*) is listed as endangered and restricted to mature and old secondary montane forests and shade coffee plantations. However, recent information about the population status and distribution of Puerto Rican Sharp-shinned Hawks is lacking. We developed a spatial geographic distribution model for Sharp-shinned Hawks in Puerto Rico from 33 locations collected during four breeding seasons (2013-2016) using biologically relevant landscape variables (aspect, canopy closure, elevation, rainfall, slope, and terrain roughness). Elevation accounted for 89.8% of the model fit and predicted that the greatest probability of occurrence of Sharp-shinned Hawk sin Puerto Rico (>60%) was at elevations above 900 m. Based on our model, an estimated 56.1 km^2 of habitat exists in Puerto Rico with a high probability of occurrence. This total represents ~0.6% of the island's area. Public lands included 43.8% of habitat with high probability of occurrence (24.6 km^2), 96% of which was located within four protected areas. Our results suggest that Sharp-shinned Hawks are rare in Puerto Rico and restricted to the higher elevations of the Cordillera Central. Additional research is needed to identify and address ecological limiting factors, and recovery actions are needed to avoid the extinction of this endemic island raptor.

Resumen

Evaluación del estado de conservación de una rapaz insular en peligro: el Gavilán estriado en Puerto Rico

El Gavilán estriado es una rapaz ampliamente distribuida en las Américas la cual tiene tres subespecies endémicas al Caribe. La subespecie endémica a Puerto Rico está listada como en peligro que se restringe a bosque montano maduro y secundario y plantaciones de café bajo sombra. La información sobre el estado poblacional y distribución del Gavilán estriado de Puerto Rico es escasa. Desarrollamos un modelo espacial de distribución geográfica del Gavilán estriado en Puerto Rico con 33 localidades de observaciones colectadas durante las temporadas reproductivas del 2013 al 2016 y variables de paisaje biológicamente relevantes (aspecto, cobertura de dosel, elevación, lluvia, pendiente y rugosidad de terreno). La elevación representó el 89.8 % del ajuste del modelo y predijo la mayor probabilidad de ocurrencia del Gavilán estriado en Puerto Rico (>60 %) se encuentra por arriba de los 900 m. El modelo estimó 56.1 km^2 de hábitat existente en Puerto Rico con alta probabilidad de ocurrencia. Este total representa 0.6 % del área de la isla. Las tierras públicas incluyeron 43.8% de hábitat con alta probabilidad de ocurrencia, del cual 96 % está localizado en cuatro áreas protegidas. Nuestros resultados sugieren que el Gavilán estriado en Puerto Rico es raro y está restringido a las elevaciones más altas de la Cordillera Central. Se necesita una mayor

investigación para abordar e identificar los factores ecológicos limitantes y acciones de recuperación son necesarias para evitar la extinción de esta rapaz insular endémica.

Introduction

Sharp-shinned Hawks (*Accipiter striatus*) are found in forested habitats of North America, Central America, South America, and the Greater Antilles (Bildstein and Meyer 2000, Ferguson-Lees and Christie 2001). Sharp-shinned Hawks in the West Indies (Friedmann 1950) are represented by three endemic subspecies, including *Accipiter s. striatus* (Hispaniola), *A. s. fringilloides* (Cuba), and *A. s. venator* (Puerto Rico). *A. s. venator* is considered a vagrant in the Virgin Islands and is listed as endangered in Puerto Rico (USFWS 1997). Breeding territories of Sharp-shinned Hawks have been reported in protected areas in the Cordillera Central, the Cayey Mountains, and Luquillo Mountains in El Yunque National Forest (Snyder and Wiley 1976, Delannoy 1984, 1997, Miranda-Castro et al. 2000). The population of these hawks in Puerto Rico was reported to have declined from about 240 individuals in 1985 to 82 during 1991 and 1992 in public lands (Delannoy 1992, 1997).

Information about the life history parameters of Sharp-shinned Hawks in Puerto Rico, including survival, movements, dispersal, habitat use, and resource selection, is limited (Delannoy 1984). Population declines usually involve documented changes in demographic parameters (e.g., survival and reproduction) and environmental factors such as habitat loss and degradation (Holmes et al. 1996). Despite legal protection, information about the status of Sharp-shinned Hawks populations in Puerto Rico has not been updated since 1992 and no meaningful conservation efforts have been implemented. Our objective, therefore, was to develop a spatially explicit habitat suitability model for

Sharp-shinned Hawks in Puerto Rico based on available macrohabitat preferences and current information about their distribution.

Methods

Study area

The island of Puerto Rico (17°45’, 18°30’ N, 65°45’, 67°15’W) is the smallest and easternmost of the Greater Antilles, encompassing an area of 8740 km^2 (Daly et al. 2003). With a predominately mountainous landscape, Puerto Rico has six bioclimatic life zones largely defined by altitude and rainfall, including subtropical dry forest, subtropical lowland moist forest, subtropical wet forest, subtropical lower montane wet forest, subtropical rain forest, and subtropical lower montane rain forest (Ewel and Whitmore 1973, Gould et al. 2008). Our study (Figure3.1) was conducted in the montane forest regions of Puerto Rico (Cordillera Central, Cayey Mountains, and Luquillo Mountains) in protected areas and surrounding private lands where Sharp-shinned Hawks have previously been reported (Delannoy 1992, 1997, Miranda-Castro et al. 2000).

The Cordillera Central, the principal montane region of Puerto Rico, is characterized by rough terrain and steep slopes with highest elevations ranging from 875 m in the western sections to1338 m on the eastern end of the mountain range. Mean annual temperatures and precipitation are affected by elevation and ranged from 18 to 25˚C. Precipitation generally increases from west to east, ranging from 234 cm to 4000 cm (Delannoy 1984, Fogarty and Vilella 2002). On the west side of the Cordillera Central, dominant overstory species include *Homalium racemosum* (Flacourtiaceae), *Micropholis chrysophylloides* (Sapotaceae), *Terebraria resinosa* (Rubiaceae), and *Linociera dominguensis* (Oleaceae). Forest canopies in the central part of the Cordillera

Central are dominated by *Micropholis chrysophylloides* (Sapotacea), *Ocotea spathulata* (Lauracea), *Prestoea montana* (Arecaceae), *Sapium laurocerasum* (Euphorbiacea), and *Tabebuia heterophylla* (Bignonacea) (Vidal and Padrón 2001, Fogarty and Vilella 2002). Forests on the eastern range of the Cordillera Central are dominated by *Prestoea montana* (Arecaceae) and other associated species such as *Buchenavia tetraphylla* (Combretaceae), *Micropholis chrysophylloides* (Sapotacea), and *Tabebuia schumanniana* (Bignonacea). At lower elevations (700–850 m), forests are dominated by *Dacryoidesexelsa* (Burseracea) (Delannoy 1997). Unmanaged timber plantations of *Calophyllum brasiliense* (Clusiaceae), *Eucalyptus robusta* (Myrtaceae), and *Pinus caribaea* (Pinaceae) occur throughout the area on several public lands.

The Cayey Mountains are located on the southeastern region of the island, where elevation ranges from 250 to 903 m, annual precipitation averages 235 cm, and temperature averages 22.4˚C. Forest overstories are dominated by *Prestoea montana* (Arecaceae) associated with *Spathodea campanulata* (Bignoniacea), *Inga laurina* (Leguminoceae), and *Ocotea leucoxylon* (Lauracea). Forests at low and mid-elevations are dominated by *Cecropia schreberiana* (Moracea) and *Dacryoidesexelsa* (Burseracea) (Lomascolo and Aide 2001).

The Luquillo Mountains (for site description see Brown et al. 1983, Scatena http//lternet.edu/sites/luq) represent the major physiographic formation of northeastern Puerto Rico where elevations range from 20 to 1080 m and mean annual precipitation from 200 to 500 cm. Annual temperatures averaged 25˚C in the lower slopes and 19˚C at higher elevations (Delannoy 1997). Some portions of the Luquillo Mountains reflect past forest disturbances from agriculture and hurricanes (Foster et al. 1999). However, the

Luquillo Mountains include the largest remaining areas of primary montane forest in Puerto Rico, located in El Yunque National Forest (Lugo 1994). The forests of the Luquillo Mountians are characterized by four dominant forest types found along an elevation gradient, *Dacryodes excels* (Burseracea) at lower elevations, *Cyrilla racemiflora* (Cyrillacea) at mid-elevations, and *Prestoea montana* (Arecaceae) and elfin wood forest on ridge tops and peaks (Scatena 1989).

Field procedures

To optimize sampling effort, we established survey points using available spatial databases to map areas of mature forest, secondary forests, and coffee plantations that met the following criteria: canopy closure > 60% using percentage tree canopy coverage (Huang et al. 2004), elevation above 350 m (NOAA 2012), and land cover types from the Puerto Rico GAP Analysis (Gould et al. 2008). To facilitate detection of Sharp-shinned Hawks, we used playback surveys, a method commonly used to attract territorial hawks in the genus *Accipiter* during the breeding season (Rosenfield et al. 1988, Kimmel and Yahner 1990, Hargis and Woodbridge 2006, Henneman and Andersen 2009). From January to April of each year, we conducted playback surveys between 06:30 and 10:30 using alarm calls of a local Sharp-shinned Hawk individual (recorded and provided by Mark W. Oberle) with a hand-held digital game caller amplifier (FoxPro® Model 48B, FoxPro Systems, Lewistown, Pennsylvania, USA) at 100–110 dB (King et al. 2011). Observers remained at each station for 20 min, beginning with 5 min without broadcasts, 5 min where playback was broadcast for 20 sec each minute, and 10 min without broadcasts (Mosher et al. 1990, King et al. 2011). From January to mid-March each year, we also conducted surveys to detect aerial displays by courting pairs to locate nesting territories (Delannoy 1984). During each survey, we recorded the azimuth to detected Sharp-shinned Hawks with a compass and distance with a rangefinder. In addition to these surveys, we conducted searches for nesting activity in 33 historical territories in Maricao and Toro Negro Forests reported previously between 1978 to 1983 (Delannoy 1984, 1992, Cruz and Delannoy 1986).

Database development and data analysis

We created a presence-only database of Sharp-shinned Hawk locations and, for analysis, considered territorial pairs as a single location. For each sighting of flying individuals, we created projected coordinates using the estimated distance and azimuth of each sighting from the observation point with the bearing distance tool in ArcMap (ESRI 2006). To model Sharp-shinned Hawk distribution, we selected biologically important environmental variables, including elevation, slope, and canopy closure (Delannoy 1984, Cruz and Delannoy 1986). We also incorporated terrain aspect and terrain roughness to describe landscape heterogeneity given its potential influence on nest habitat characteristics (Boose et al. 2004, Flynn et al. 2010, Korzeniowska and Korup 2016). Because periods of continuous rains may negatively affect the early nestling stages of *Accipiter* hawks, we incorporated total rainfall during the nesting and fledgling period (April to May; Snyder and Wiley 1976, Delannoy and Cruz 1988, Mearns and Newton 1988).

We obtained elevation data (30-m resolution) from the Puerto Rico Digital Elevation Model (DEM) (NOAA 2012). We derived models of slope and aspect directly from the DEM using respective Spatial Analyst extension in ArcMap (ESRI 2006) and our terrain roughness model was derived from our slope model by calculating the variety statistic of a 3-by-3 rectangle using the Focal Statistics extension in ArcMap (ESRI 2006). We used kriging interpolation with the Geostatistical Analyst Tool in ArcMap (ESRI 2006) for short-term average (2010 – 2015) of total rainfall during April and May using available data of 50 weather stations within the overall study, including 46 NOAA stations (http://www.ncdc.noaa.gov/cdo-web/datatools/findstation), three stations from the Southeast Regional Climate Center (http://www.sercc.com/), and one located at the El Verde Biological Station (http://evfs.ites.upr.edu/research/meteorological-data) in El Yunque National Forest. We also used a forest-canopy digital model developed for Puerto Rico to account for canopy closure at each sighting location (Huang et al. 2004).

We used MaxEnt version 3.3.3 (https://www.cs.princeton.edu/~schapire/maxent/) based on Sharp-shinned Hawk locations and environmental covariates to develop a geographic distribution model. Maximum entropy modeling is a machine learning approach designed to derive solutions based on conditional data and in an ecological context, is based on the principle that a species' distribution can be modeled based on relevant ecological constraints while avoiding unfounded variables (Phillips et al. 2006, Pearson et al. 2007). MaxEnt models perform well on datasets characterized by small samples and correlated variables (Hernández et al. 2006, Elith et al. 2011). As suggested by Phillips et al. (2006), we used the recommended default values for the convergence threshold (0.00001) and a maximum of 1000 iterations. Theoretically, any pixel with a probability > 1% is considered suitable (Phillips et al. 2006), however, for visualization purposes, we binned probability of occurrence into four categories, including very low (<9%), low (10 – 39%), medium (40 – 59%), and high (60 – 100%).

We used receiver operating characteristic (ROC) analysis to evaluate the predictive ability of the model. This graphical approach is used to illustrate performance of a binary classifier at varying discrimination thresholds (Phillips et al. 2006, Pontius and Parmentier 2014). Receiver operating characteristics quantify model performance for all probability thresholds using the values associated with the area under the curve (AUC). We evaluated the usefulness of the model according to Swets (1988) as very good (AUC= > 0.9), good (AUC= 0.7 – 0.9), or poor (AUC= < 0.7). The ROC method plots sensitivity values (true positive fractions) against the fractional predicted area (false-positive fraction), then compares the pattern observed in the model to a randomly generated pattern (Phillips et al. 2006). For model evaluation, we randomly assigned 25% of Sharp-shinned Hawk locations as test data and the remaining 75% were training data to generate the area under the ROC plot (Guisan and Zimmermann 2000, Phillips et al. 2006). Finally, we used a jackknife approach to evaluate importance of variables in model performance (Phillips et al. 2006). Values are presented as means ± 1 SE.

Results

We established a network of 21 overlooks and 116 calling stations in the Maricao Commonwealth Forest and adjacent private areas during 2013 and visited calling stations monthly from January to April. Additionally, observers invested 179 h searching for nesting activity in historical territories identified by Delannoy (1984). In 2014, we conducted aerial display surveys at 37 overlooks and 139 calling stations in the central and eastern part of the Cordillera Central, Cayey Mountains, and Luquillo Mountains. Finally, we conducted aerial display searches at 52 observation points in the eastern part of the Cordillera Central and Cayey Mountains during 2016. We recorded 51 SSHA, 18 territorial pairs, and 15 unpaired individuals at 33 locations. Twenty-seven detections were on private lands and 24 were in forest reserves, with territorial pairs found equally among private and public lands (Appendix B). Elevation of Sharp-shinned Hawk locations averaged 884 ± 176 m (range = 393 – 1226 m), canopy closure averaged 64 ± 11% (range = 31 – 77%), and were characterized by steep slopes averaging 19 ± 5˚ (range = 11 – 33˚).

The area under the ROC curve for training (0.99) and test data (0.97) suggested variables used were good predictors of Sharp-shinned Hawk occurrence. Elevation accounted for 90% of the model fit, terrain roughness contributed 4.5%, and remaining variables accounted for 5.5% (Table 3.1). The resulting model indicated a relatively small portion of the total area of the island (56 km^2) was classified as high probability of occurrence. Another 85 km^2 were classified as medium probability and the remaining area of the island was classified as low probability (Table 3.2). The model indicated that the area of Puerto Rico with the greatest probability of occurrence was the central region of the Cordillera Central, mostly in and around the forest reserves of Toro Negro and Tres Picachos (Figure 3.2). Most habitat classified as high (3,152 ha) and medium (6,298 ha) probability of occurrence for Sharp-shinned Hawks was on private lands (Table 3.2). Areas with a high probability of occurrence in protected areas included Toro Negro Forest (1511 ha), Tres Picachos Forest (426 ha), Guilarte Forest (314 ha), and El Yunque National Forest (104 ha). Conversely, areas with a medium probability of occurrence (Table 3) included some of these same reserves, namely Toro Negro Forest (630 ha), Guilarte Forest (634 ha), Tres Picachos Forest (344 ha), El Yunque National Forest (315 ha), Carite Forest (144 ha), and Maricao Forest (123 ha).

Discussion

The MaxEnt model identified the distribution of Sharp-shinned Hawks in Puerto Rico centered on the central and eastern regions of the Cordillera Central, including a number of forest reserves and private lands. Areas of medium and high probability of occurrence were limited to the eastern Cordillera Central, Cayey Mountains, and Luquillo Mountains. Model results coincided with the distribution of location records previously reported. The location of 13 active territories recorded in our study agreed with previous studies, 6 were found in or nearby the forests of Toro Negro, 4 in Maricao, 2 in Guilarte, and one in Carite, and additionally 3 single individuals in Toro Negro and one in Tres Picachos forests (Cruz and Delannoy 1986, Delannoy 1992, 1997, Miranda-Castro et al. 2000).

Improving distribution models and associated predictions provides information on the status of a species and represent additional conservation tools for decision makers (Webb et al. 2014). The MaxEnt model here presented represents an improvement over previous estimates of predicted Sharp-shinned Hawk habitat derived using land cover (vegetation type and canopy closure) and elevation, instead considering actual locations of Sharp-shinned Hawks territories to develop a predictive outcome as presented by Jiménez et al. (2006). Our model results suggested a contraction in the geographic range of this endangered island raptor, with the area of greater occurrence (≥ 60%) representing only 0.6% of Puerto Rico and restricted to higher elevations. The pattern described by the model was similar to other declining island species such as ‘akikiki (*Oreomystis bairdi*) and ‘akeke‘e (*Loxops caeruleirostris*) and other Hawaiian forest endemics currently restricted to higher elevations as a result of poor survival conditions in the lowlands

(Fortini et al. 2015, Paxton et al. 2016). Delannoy (1997) suggested a 46% decline in six-year period (1985-1991) of the Sharp-shinned Hawk populations in forest reserves of Puerto Rico. Our findings highlight the critical conservation status of Sharp-shinned Hawks based on a restricted geographic range coupled with traits associated with extinction risk, such as a small and declining population (Purvis et al. 2000, Krüger and Radford 2008).

Elevation best explained the distribution of Sharp-shinned Hawks in Puerto Rico, with the greatest probability of occurrence (>60%) at elevations above 900 m (Figure3.3 and Figure 3.4). Previous research in Maricao Forest documented up to 32 SSHA nesting sites at elevations of 350 to 810 m (Delannoy 1984, Cruz and Delannoy 1986). However, despite surveying historical territories and private lands at elevations of 350 m and above, we recorded 69% of Sharp-shinned Hawk sightings and 72% of territorial pairs above 800 m. Parasitism of nestlings by botflies (*Philornis* spp.) and predation of eggs and young by Pearly-eyed Thrashers (*Margarops fuscatus*) have been reported to negatively impact Sharp-shinned Hawk reproduction. Delannoy (1984) reported that botfly parasitism caused almost 40% of nest failures and 61% mortality of chicks in Maricao Forest. Further, circumstantial evidence of predation of Sharp-shinned Hawkeggs and nestlings by Pearly-eyed Thrashers accounted for 29% of nest failures in the Luquillo Mountains (Wiley 1986). Recent information is available concerning botfly parasitism (R. Thorstrom pers. comm.) and potentially Sharp-shinned Hawk nest predation by Pearly-eyed Thrasher in the Cordillera Central region. However, we have no way to ascertain whether the current displacement of these hawks to higher elevations is in response to these ecological pressures or habitat related factors. However, the abundance of Pearly-eyed Thrashers and rates of botfly infestation may decrease with elevation (Young 1993, Arendt 2006).

Animal populations are generally less abundant at the periphery of their geographic ranges because of ecological factors that may reflect the intrinsic tolerance limits of organisms (Gaston 1990, Brown et al. 1995). Moreover, the dimensions of geographic ranges are dynamic and may rapidly respond to changing conditions (Gaston 2003). The Maricao Forest was at one time the center of distribution for Sharp-shinned Hawk in Puerto Rico, but they are presently restricted to the higher-elevation sections of the reserve, amounting to 1.7% of the area (Delannoy 1997). Similarly, the distribution and abundance of these hawks in the Luquillo and Cayey Mountains have experienced major declines (Delannoy 1997). Snyder et al. (1987) reported 10 nesting territories and estimated that ~50 Sharp-shinned Hawks were present in El Yunque National Forest during the 1970s and 1980s. However, we did not detect any Sharp-shinned Hawks in El Yunque and recorded only one sighting in the Cayey Mountains.

Our distribution model suggests that remaining predicted habitat suitable for Sharp-shinned Hawks has become increasingly isolated in the mountain ranges of Puerto Rico. During the past 60 years, Puerto Rico experienced the abandonment of agriculture and expansion of urban areas (López et al. 2001, Grau et al. 2003). Urban expansion may have exacerbated the isolation of suitable habitat as road infrastructure and urban centers have expanded in the interior regions of the island (Grau et al. 2003). The eastern and east-central regions of Puerto Rico have undergone increased rates of urban development near protected areas (e.g., El Yunque and Carite Forest), coinciding with the areas with where Sharp-shinned Hawks are no longer present (Delannoy 1997, Castro-Prieto et al. 2017).

Hurricanes constitute a major disturbance to terrestrial ecosystems in the Caribbean islands and their effects play a major role in forest succession. Hurricanes can affect forest wildlife through effects on population size and rates of change, as well as changes in supporting habitat structure (White et al. 2005, Flynn et al. 2010). Further, forest-specialist birds may shift habitat use patterns after hurricanes (White et al. 2005, Flynn et al. 2010). During September 1998, Hurricane Georges moved east to west across the Cordillera Central causing damage and alteration of forest structure, including loss of tree branches (e.g., nesting structures) and the opening of the forest canopy with a consequent increase in understory and midstory cover (Wiley and Wunderle 1993, Vilella and Fogarty 2005, Flynn et al. 2010, Wunderle and Arendt 2011). Consequently, post-hurricane forest conditions may have reduced their value as suitable habitat for Sharp-shinned Hawks (Tossas 2006).

The spatially disjointed distribution of remaining habitat places an additional burden on the long-term survival of Sharp-shinned Hawks in Puerto Rico. This degree of isolation of habitat with high probability of occurrence may reduce spatial connectivity of populations (e.g., Luquillo Mountains with the Cordillera Central) and negatively influence dispersal of juveniles following the post-fledging dependency period and adults seeking new nesting territories or mates (Betts et al. 2007, Braunisch et al. 2010). No information is available concerning movement patterns of Sharp-shinned Hawks in Puerto Rico. Anecdotal evidence from nestlings and adults in Maricao Forest indicates a minimum movement of 1.7 km from nest sites and switched territories (Delannoy 1984, 2015 pers. comm.). The boundaries of the breeding territories of other island raptors, such as Galapagos Hawks (*Buteo galapagoensis*), Hawaiian Hawks (*B. solitarious*), and Puerto Rican Broad-winged Hawks (*B. platypterus brunnescens*) overlap and natal dispersal distances are limited (e.g., <4 km; Clarkson and Laniawe 2000, Vilella and Hengstenberg 2006, Rivera et al. 2011).

In Puerto Rico, no information is available concerning the demography and spatial dynamics of Sharp-shinned Hawks, preventing reliable inference on the contribution of the aforementioned limiting factors on the population status and viability of this endangered subspecies of oceanic island raptor. The likelihood of recovery for an endangered species is assumed to be proportional to the time since listing has occurred, with an average peak in improvement of ~12 to 13 years after listing (Male and Bean 2005, Taylor et al. 2005). However, the Sharp-shinned Hawk has been listed since 1994 and yet the status of the species appears to be more precarious today (USFWS 1994, 1997). Our results suggest recovery actions are a priority for the Sharp-shinned Hawk.

Efforts to quantify life history parameters and annual cycle processes of Sharp-shinned Hawks in Puerto Rico is urgently needed to better understand the factors behind the observed population decline and geographic range contraction (Jachowski et al. 2015). Reintroductions and translocation have previously been used successfully to restore populations of island raptors. Captive breeding and reintroduction of Mauritius Kestrels (*Falco puncatus*) resulted in a population increase from four to 400 individuals in a 23-year period (Safford and Jones 1997). However, limiting factors need to be identified and addressed before translocations and reintroductions are attempted (Jachowski et al. 2015).

The use of models to predict geographic distribution can be a useful tool in conservation by providing information on potentially occupied areas and highlighting geographic regions of importance for conservation planning (Pearce and Boyce 2006, Phillips et al. 2006). Our results provide information about the location of remaining populations of Sharp-shinned Hawks in Puerto Rico and potential sites for reintroduction and translocation. Most importantly, our model results identified private lands where habitat protection and management actions may be directed. Future recovery actions must prioritize coordination and collaboration with private landowners in areas occupied by Sharp-shinned Hawks to deploy effective habitat conservation strategies. Landscape conservation design projects like the Bosque Modelo of Puerto Rico may play important roles in the conservation of Sharp-shinned Hawks. This project is a collaborative initiative of private landowners, non-governmental organizations (e.g., Casa Pueblo), and government organizations to establish a biological corridor connecting ecosystems across the western portion of the island (Senado de Puerto Rico 2014). The area identified by our model as having a high probability of occurrence of Sharp-shinned Hawks is located within the proposed boundaries of the Bosque Modelo.

On 20 September 2017, Hurricane Maria moved across the island of Puerto Rico from southeast to northwest with sustained winds of 250 km/hr. As of this writing, no assessments had been made of habitats nor wildlife species. However, initial reports from the center of the region identified by our model as having a high probability of occurrence for the Sharp-shinned Hawk indicate massive and extensive damage to forest cover, including defoliation and loss of canopy. Approximately 80 - 90% of the canopy at Toro Negro Forest and surrounding areas had been lost (G. Hernández, DNER Toro

Negro Forest, pers. comm.). What the impacts of this hurricane, which affected the entire island, will be on the already declining population of the Sharp-shinned Hawk are unknown. However, it is very likely that the short-term loss of suitable forest habitat, fluctuations of forest bird prey species, and incidence of parasitism by botflies on nestlings, may result in an increasingly deteriorating situation for this endangered insular raptor. Nevertheless, the information provided by our model may be particularly timely for biologists tasked with the post-hurricane response, and may help guide specific conservation actions designed to avoid the extinction of the Sharp-shinned Hawk in Puerto Rico.

Table 3.1 Selected environmental variables and their percentage contribution to the predicted potential suitable habitat for the Puerto Rican Sharp-shinned Hawk (*Accipiter striatus venator*) in Puerto Rico, 2013–2016

Environmental Variable	**Percentage contribution**	**Source/Reference**
Elevation	89.8%	NOAA (2012)
Roughness	4.5%	NOAA (2012)
Canopy closure	3.3%	Huang et al. 2004
Aspect	1.3%	NOAA (2012)
Rainfall	1.1%	NOAA, SRCC, and El Verde Biological Station
Slope	0%	NOAA (2012)

NOAA, National Oceanic and Atmospheric Administration; SRCC, Southeast Regional Climate Center.

Table 3.2 Probability of occurrence of Puerto Rican Sharp-shinned Hawk (*Accipiter striatus venator*) in private and protected areas of Puerto Rico, 2013–2016.

Probability	**Total predicted area (km^2)**	**Protected areas (km^2)**	**Private areas (km^2)**
Very low (<9%)	8,325.81 (94.1%)	182.88 (2.2%)	8,142.93 (97.8%)
Low (10-39%)	380.64 (4.3%)	61.03 (16%)	319.61 (84%)
Medium (40-59%)	85.40 (1%)	22.42(26.3%)	62.98 (73.8%)
High (60-100%)	56.09 (0.6%)	24.57 (43.8%)	31.52 (56.2%)

Table 3.3 Probability of occurrence of Puerto Rican Sharp-shinned Hawk (*Accipiter striatus venator*) in protected areas of Puerto Rico, 2013–2016.

Protected Area	**Management**	**High[a] (%)**	**Medium[b] (%)**	**Low[c] (%)**	**Very low[d] (%)**
Toro Negro Forest	DNER[e]	61.5%	28 %	8.6%	2.9%
Tres Picachos Forest	DNER[e]	17.3%	15.3%	11.2%	3.5%
Guilarte Forest	DNER[e]	12.8%	28.3%	12.2%	0.4%
El Yunque National Forest	USFS[f]	4.2%	14.1%	26.3%	52.2%
Maricao Forest	DNER[e]	1.7%	5.5%	11.6%	17.7%
Carite Forest	DNER[e]	1.4%	6.4%	23.1%	6.1%
La Olimpia Forest	CP[g]	0.5%	1.2%	1.2%	0.4 %
Foreman Conservation Easement	CT[h]	0.4%	0.2%	0	0
Finca Ledesma Moulier Conservation Easement	CT[h]	0.1%	0.2%	0.1%	0
Cerro Las Planadas Natural Reserve	DNER[e]	0	0.5%	3.1%	4.2%
Las Piedras del Collado Natural Reserve	DNER[e]	0	0.1%	0.1%	0
Protegida Marueño Natural Reserve	CT[h]	0	0	0.2%	1.1%
Protegida La Robleda Natural Reserve	CT[h]	0	0.1%	0. %	0.3%

Table 3.3 (continued)

Protected Area	**Manag.**[1]	**High**[2]	**Med.**[3]	**Low**[4]	**V. low**[5]
Bosque del Pueblo de Adjuntas	CP[g]	0	0	0.6%	1.8%
Guayama Experimental Forest	FS-IITF	0	0	0.3%	0.6%
Sistema de Cuevas y Cavernas de Aguas Buenas Natural Reserve	DNER[e]	0	0	0	3.9%
Cañón San Cristóbal Natural Protected Area	CT[h]	0	0	0.2%	3.4%
Jorge Sotomayor del Toro Natural Protected Area	CT[h]	0	0	0.1%	0
Ulpiano Casal Natural Protected Area	CT[h]	0	0	0.1%	0.7%
Siembra Tres Vidas Conservation Easement	Conservation Trust	0	0	0	0
Finca Jájome Natural Protected Area	Conservation Trust	0	0	0.2%	0.7%
Culebras Natural Protected Area	Conservation Trust	0	0	0.1%	0

[a] 60–100 % probability of occurrence probability; [b] 40–59%probability of occurrence; [c]10–39% probability of occurrence; [d] <9% probability of occurrence; [e] Department of Natural and Environmental Resources of Puerto Rico; [f] United States Forest Service; [g] Casa Pueblo Foundation; [h] Conservation Trust of Puerto Rico; [I] United States Forest Service-International Institute of Tropical Forestry.

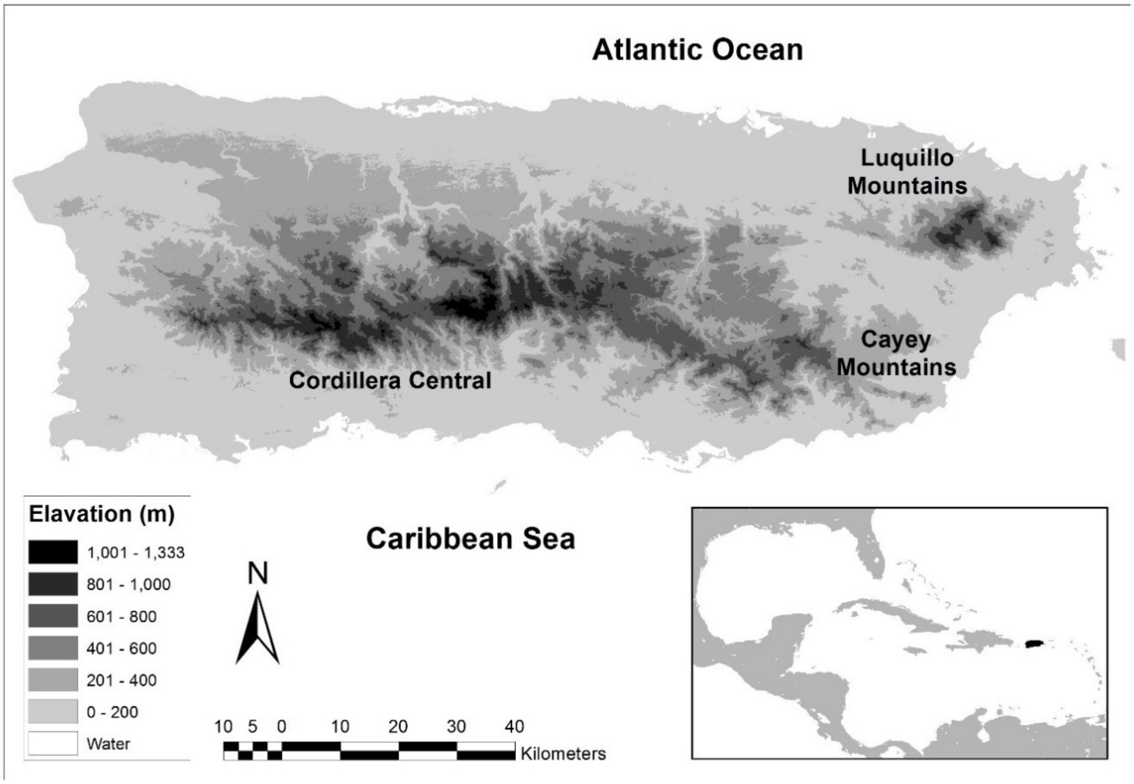

Figure 3.1 Map of Puerto Rico indicating major mountain formations and location in the Caribbean archipelago (inset).

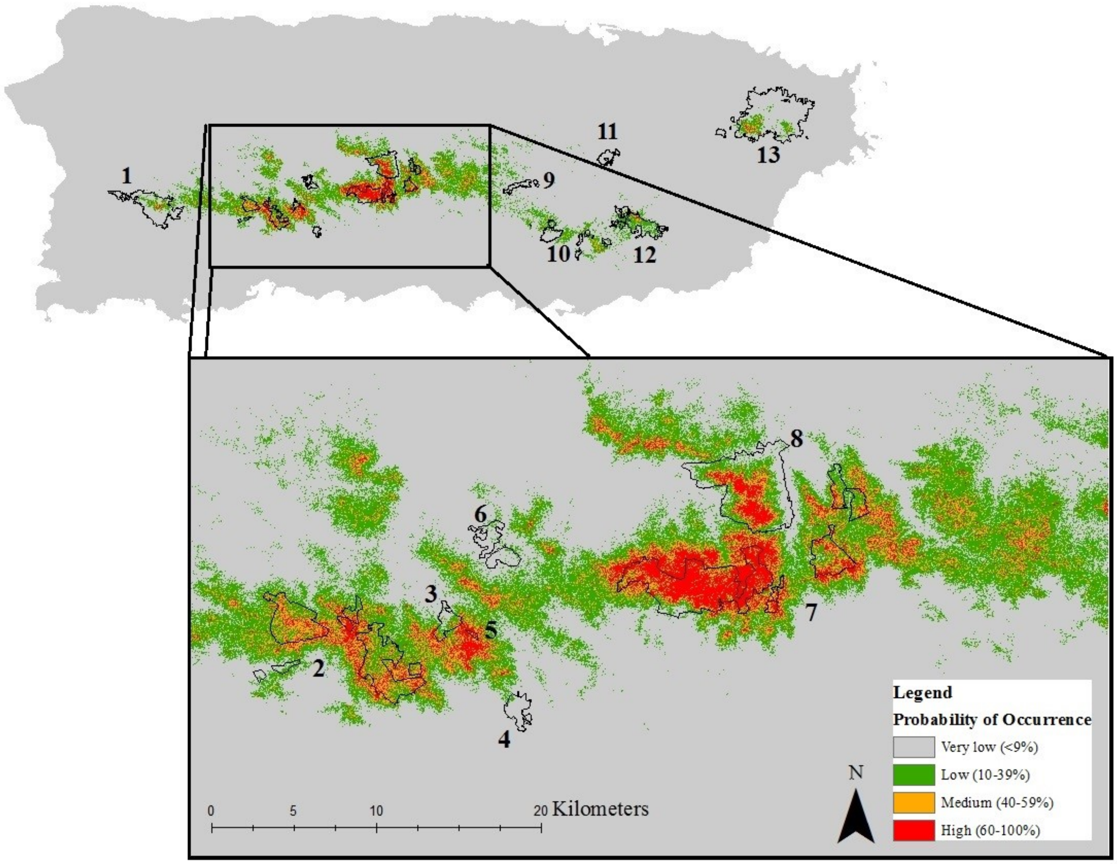

Figure 3.2 Predicted suitable habitat (2013–2016) for Puerto Rican Sharp-shinned Hawk (*Accipiter striatus venator*) in Puerto Rico. Protected areas with occurrence probability > 10 % include: Maricao Forest (1), Guilarte Forest (2), Bosque la Olimpia (3), Mureño Protected Area (4), Foreman Conservation Easement (5), Bosque del Pueblo (6), Toro Negro Forest (7), Tres Picachos Forest (8), Cañón de San Cristobal Protected Area (9), Cerro Las Planadas Natural Reserve (10), Aguas Buenas Caverns Natural Reserve (11), Carite Forest (12), and El Yunque National Forest (13).

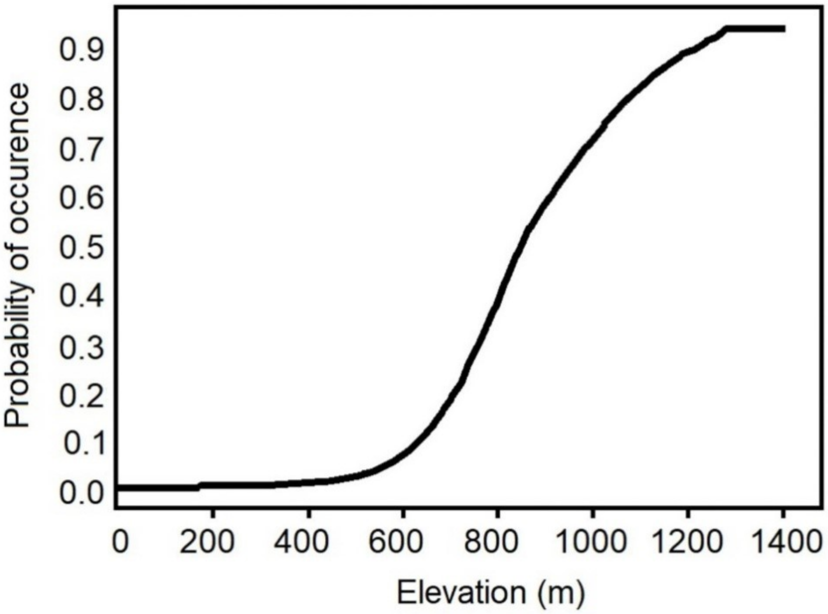

Figure 3.3 Response curve of elevation and predicted probability of occurrence of Puerto Rican Sharp-shinned Hawk in Puerto Rico, 2013–2016.

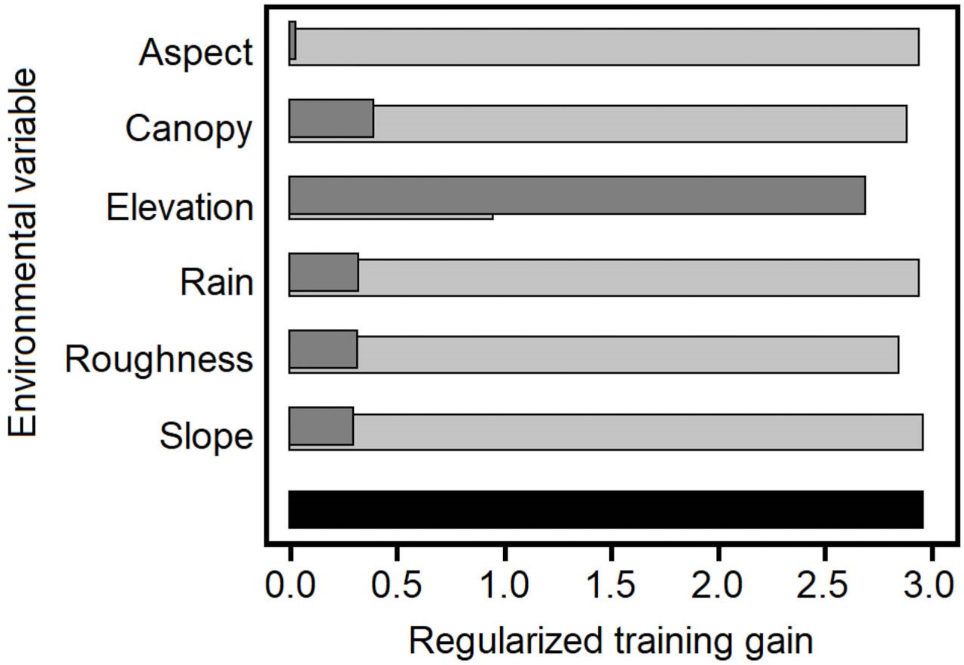

Figure 3.4 Jackknife test of relative importance of environmental variable predictors for Puerto Rican Sharp-shinned Hawk relative to all environmental variables (black bar), without a specific predictor variable (light gray), and with only a specific variable (dark gray bar). See Methods for descriptions of environmental variables.

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CHAPTER IV

A SEASONAL POPULATION MATRIX MODEL OF THE CARIBBEAN RED-TAILED HAWK BUTEO JAMAICENSIS JAMAICENSIS IN EASTERN PUERTO RICO

This chapter was submitted to the International Journal of Ornithology (Ibis) and is currently under review.

Abstract

Reliable estimates of life history parameters and their functional role in animal population trajectories are critical, yet often missing, components in conservation and management. We developed seasonal matrix population models of the Red-tailed Hawk in two regions of the mountains of eastern Puerto Rico, to describe the influence of early life stages (nestling and clutch survival) on population growth. Modeled populations exhibited positive discrete rates of growth in both Modeled populations exhibited positive discrete rates of growth in forest above 400 m (λ highlands = 1.05) and in forest below 400m (λ lowlands = 1.27) of the Luquillo Mountains. Further, adult survival was the most important parameter influencing population growth (elasticity highland forest = 0.86, elasticity lowland forest = 0.53). Besides survival of adults, nestling survival had a greater influence on λ than did other life stages (sensitivity lowlands = 0.46, sensitivity highlands = 0.48), stressing the importance of this life stage for the population growth rate of Red-tailed Hawks in our study area. Seasonal matrices are rarely used to describe the dynamic of bird populations. However, these can be a useful tool to analyze the influence of life stages in the annual cycle to better address conservation and management efforts, especially for sedentary species such as those inhabiting oceanic islands.

Keywords: Caribbean, population analysis, elasticity analysis, sensitivity analysis, seasonal matrix, islands.

Introduction

Density-dependent and density-independent factors can affect animal demography, with consequent effects on population growth (Elton 1924, Nicholson 1933, Andrewartha & Birch 1954, Sæther & Bakke 2000, Coulson *et al.* 2001, Katzner *et al.* 2007). Individuals at different life stages may respond differently to the same stressor, resulting in differing survival rates and contributions to population growth (Sæther & Bakke 2000, Coulson *et al.* 2001). There is limited information on the population dynamics of tropical and insular raptor species (Newton 1979, Sæther & Bakke 2000, Katzner *et al.* 2006). Early life stages may be particularly important to the demography of species characterized by closed populations or limited immigration rates, typical of island populations (Manlik *et al.* 2016, McGrady *et al.* 2017).

Early life stages can play an important role in defining the population trajectory and adaptations of an island colonizer. Populations of species in the early stages of island colonization may undergo an early phase of logarithmic growth resulting from a greater intrinsic rate of population increase because of greater reproduction and survivorship (MacArthur & Wilson 1967, Gotelli 2008). Following a successful colonization, some species may evolve island traits with associated lesser vital rates while retaining greater values of adult and juvenile survival (MacArthur & Wilson 1967). Therefore, parameters driving population dynamics on islands may contribute differently to population growth compared to mainland populations (Newton 1998, Sæther & Bakke 2000, Gotelli 2008).

The life histories of oceanic island species are shaped by selective pressures that may result in adaptations to exploit multiple resources, including niche expansion or shifts due to release from interspecific competition (Crowell 1962, MacArthur *et al.* 1972, Abbott 1980, Baker-Gabb 1986, Blondel 2000). Island species are exposed to local stochastic events (e.g. hurricanes) or different predation rates that potentially affect survival rates, reproduction and population growth at a local scale (Brown 1969, MacArthur *et al.* 1972, Cody 1985, Newton 1998, Brown 1995, Johnson 2007). Along with nest predation, weather is one of the most important factors of nest failure for tropical raptors, decreasing breeding success (Whitacre & Burnham 2012). The impact of breeding success on population growth of island raptors is poorly known, mostly due to lack of information about early life stage survival (Klavitter *et al.* 2003).

The Red-tailed Hawk *Buteo jamaicensis* has been well studied in temperate environments, but information is limited from Neotropical populations. In Puerto Rico, the Caribbean Red-tailed Hawk *Buteo j. jamaicensis* exhibits typical island traits such as extensive spatial overlap among individual territories and greater population density than mainland conspecifics (Santana *et al.* 1986, Santana & Temple 1988, Boal *et al.* 2003, Nimitz 2005, Llerandi 2006). Both greater abundance and spatial overlap might increase hierarchy and agonistic interactions among conspecifics, resulting in individuals displaced to territories of lesser quality, resulting in reduced breeding success and local population growth (Ferrer & Donazar 1996, Rodenhouse *et al.* 1997).

Raptors play important roles in oceanic islands as the top consumers given the absence of native mammalian ground predators. Red-tailed Hawks consume a wide diversity of prey in Puerto Rico (Snyder *et al.* 1987, Santana & Temple 1988, White *et al.* 2005, Llerandi 2006), including other raptors (e.g. Puerto Rican Short-eared Owl *Asio flammeus portoricensis*), birds (e.g. Puerto Rican Parrot), reptiles (e.g. Puerto Rican Boa *Chilabothrus inornatus*), land crabs *Cardisoma guanhumi* and invasive mammals (e.g. rats *Rattus spp.*, small Indian mongoose *Herpestes auropuncatus*). Despite their ecological relevance, the population dynamics of island raptors remains poorly understood, potentially limiting the reach of conservation and management measures.

Matrix population models are used to quantify demographic parameters and assess their functional role in population dynamics (Leslie 1945, Caswell 2001, Beissinger *et al.* 2006). Traditional matrix population model structure commonly represents changes in fixed time periods (e.g. annual changes) but cannot be used to model changes across time periods of varying length (Caswell 2001, Caswell & Shyu 2012). In contrast, seasonal matrix models divide the year into a series of phases or transitions to incorporate variability of vital rates estimated over intervals shorter than a year (e.g. incubation) and integrate them in a full annual-cycle population model (Caswell 2001). Therefore, seasonal matrix models can be a useful tool to evaluate early life stage changes of island raptor populations characterized by regional differences in survival (Petty 1992, Taylor 1994, Rohner 1996, Newton 1998).

Understanding how population growth of a resident species is influenced by individual life stages is necessary to develop full annual-cycle models. The Red-tailed Hawk in Puerto Rico is probably the best know tropical island form of this widely distributed species, thus a practical subject to assess the relationship of vital rates to population growth in an insular environment (Santana & Temple 1988, Boal *et al.* 2003, Nimitz 2005, Llerandi 2006, Vilella & Nimitz 2012). Island population traits of the Red-tailed Hawk in Puerto Rico may play an important role in breeding success with a direct impact on population growth. In this study, we predicted changes in population growth and associated vital rates would vary among Red-tailed Hawks at different elevations. We developed a seasonal matrix model to estimate the influence of life stages on the rate of finite population increase (λ) on the Red-tailed Hawk, how island rates may vary from mainland conspecific populations, and how this informs our understanding of the ecology of island raptors generally.

Methods

Puerto Rico and its satellite islands (17°45’ 18°30’ N and 65°45’, 67°15’W) represent the smallest and easternmost of the Greater Antilles and comprise 8,740 km^2 (Daly *et al.* 2003). The landscape is predominately mountainous (Gould *et al.* 2007). The Luquillo Mountains are located in northeastern Puerto Rico, where elevations range from 0 to 1,080 m and mean annual precipitation increases from 100 to 500 cm with elevation (Delannoy 1997, Vilella & Nimitz 2012). The lowland forest (lowland moist forest) was characterized by a mosaic of second growth semi-deciduous forest of different stages, pastures and abandoned crop lands. Lowland moist forest was found at elevations of 0 to 400 m with an average annual precipitation of 100 to 220 cm. The highland forest (subtropical wet forest and lower montane wet forest) was located above 400 and annual rainfall averaged 200 to 500 cm. Highland forest was characterized by mature and old second-growth broadleaf tropical forests with a continuous canopy (Ewel & Whitmore 1973).

The Red-tailed Hawk includes resident tropical populations in Central America and the Caribbean islands (Preston & Beane 1993). In Puerto Rico, the Red-tailed Hawk is found across the island and its abundance is one of the highest recorded along the species' distribution (Nimitz 2005, Llerandi 2006). The Red-tailed Hawk in Puerto Rico exhibits typical island traits (e.g. niche expansion, high territory overlap, high survival rates), but vital rates are more comparable with mainland populations than to other insular raptors (Preston & Beane 1993, Nimitz 2005, Llerandi 2006). Greater abundance and use of a wide range of habitats of varying quality may consequences for local breeding success and consequently, population growth. Santana and Temple (1988) reported differences in nestling and fledgling survival of Red-tailed Hawks among lowland and higher elevation forests in Puerto Rico.

Using demographic information on the Red-tailed Hawk in the Luquillo Mountains from Nimitz (2005) and Santana and Temple (1998), we developed separate seasonal matrix models that included five life history stages and associated transition and survival probabilities for the highlands and lowlands of eastern Puerto Rico (Table 4.1). We assumed equal sex ratios for our focal population based on previous information on ratios of some insular *Buteo* species being close to 1:1 (Newton 1979, Santana & Temple 1988, Klavitter *et al.* 2003, Woolaver *et al.* 2013). We estimated clutch size (Cl) by multiplying the average clutch size in Puerto Rico (2.3 eggs) by 0.5 to account for female-only values (Santana & Temple 1988). Clutch survival (S1) was estimated by the proportion of eggs hatched. Santana and Temple (1988) reported Red-tailed Hawk nestling survival averaged 0.7 in the highlands and 1.5 in the lowlands of the Luquillo Mountains. Therefore, we calculated nestling survival probability (S2) by estimating percentage of fledglings by clutch size, yielding 0.3 ($S2_h$) for the highlands and 0.65 ($S2_l$) in the lowlands. Finally, we used survival probabilities reported by Nimitz (2005) from radio-marked individuals in the Luquillo Mountains for juveniles (0.95), second-year birds and adults (0.97), no sex differences were indicated.

We arranged the estimated values of individual life-history transitions (e.g. egg to nestling, nestling to fledgling) into four matrices (Figure4.1) following the breeding phenology of the Red-tailed Hawk reported by Santana and Temple (1988). These included (i) Transition 1, transition of juveniles to second-year birds (S5) and a breeding period that included adult survival (S4) and clutch size (Cl); (ii) Transition 2, transition through the incubation period and clutch survival (S1); (iii) Transition 3, transition through the nestling stage and nestling survival (S2); and (iv) Transition 4, transition from fledging to juvenile (first-year, S3).

We calculated elasticity and sensitivity values in each transition matrix to estimate the effects of life stages on the population growth rate (λ) of the Red-tailed Hawk in eastern Puerto Rico using permutational eigen decomposition of the transition matrices (Caswell 2001). Elasticity is defined as the proportional relative importance of each life stage on each transition to λ, where proportional values range from 0.00 (low relative importance to) 1.00 (high relative importance, Caswell 2001). We reported elasticity values to estimate the proportional effect of each life stage on λ and sensitivity values to identify what life stage most contributed to λ and how susceptible it was to changes in different vital rates (Gotelli 2008). Sensitivity is defined as the direct relative contribution of each life stage to λ (Caswell 2001, Stevens 2009). We used the logarithmic equation $r = \text{In}(\lambda)$ to calculate the instantaneous rate of increase (r) of the Red-tailed Hawk in the highlands and lowlands (Gotelli 2008). Parameter (λ, r) estimates and matrix models were implemented in program R version 3.2.3 R (R Core Team 2014). We did not model the effects of density dependence or environmental or demographic stochasticity on the population.

Results

Adult survival had a greater proportional effect on Red-tailed Hawk population growth in the lowlands and highlands of eastern Puerto Rico. The effect of proportional change in λ of adult survival in the highlands was the same (elasticity = 0.86) during the incubation (Transition 2), nestling period (Transition 2) and was greater than the egg laying phase (Transition 1; elasticity = 0.73). In the lowlands, the effect of proportional change in λ on adult survival was the same (elasticity = 0.77) during the incubation (Transition 2), nestling period (Transition 2) and was greater than the egg laying phase (Transition 1; elasticity = 0.53). Meanwhile, the effect of proportional change in λ of second year birds in the highlands, fecundity, clutch survival and nestling survival was the same for each stage (elasticity highlands = 0.14; elasticity lowlands = 0.23) (Table 4.2). In both highlands and lowlands, adult survival had greater sensitivity values than any other life stage, which explain that λ is more sensitive to changes on this parameter. However, sensitivity for nestling survival was 0.48 in highlands and 0.38 in lowlands, suggesting that λ is most sensitive to this life stage after adult survival. In eastern Puerto

Rico, Red-tailed Hawks nesting in highlands exhibited annual rate of increase of approximately 5% (λ = 1.05, r = +0.05) and 27% in those nesting in the lowlands (λ = 1.27, r = +0.24).

Discussion

Our results indicated adult survival of Red-tailed Hawks in eastern Puerto Rico was the parameter of greatest relative importance in each transition. Adult survival accounted for 5.0% in the lowlands and 8.6% in highlands at a 10% rate of change in λ. Our findings were consistent with those reported for other birds of prey such as Red Kite *Milvus migrans*, Imperial Eagle *Aquila helaica* and the Hawaiian Hawk *Buteo solitarius*, where adult survival had a greater importance to overall population growth (Klavitter *et al.* 2003, Katzner *et al.* 2006, Sergio*et al.* 2011). Adult survival rate is a major component shaping the trajectory of breeding populations of many vertebrate species (Sæther & Bakke 2000). However, parameter λ was lower in the highlands than in lowlands. Beyond adult survival, estimates of λ were more sensitive to changes during the nestling stage in both highlands and lowlands. Therefore, early life stage transitions may have a greater influence on population growth, especially during periods of high mortality or following stochastic events such as a major hurricane (Sergio *et al.* 2011).

Local conditions and stochastic density-independent events (e.g. prolonged rain episodes) can locally influence bird populations (Elkins 1983, Newton 1998). Breeding success in birds of prey can be particularly vulnerable to severe weather events that directly affect early life stages by reducing parental care, suppressing hunting behavior or prey availability and exposing nest contents to inclement weather (Elkins 1983, Newton 1998, Sæther *et al.* 2004, Wilson & Martin 2012, Newton 2013). In the highland forests of the Luquillo Mountains, Santana and Temple (1988) reported greater reduction in parental care and suppression of hunting behavior compared to the lowland forest during periods of high precipitation or prolonged fog periods, with a consequent greater nestling mortality. Elasticity values of the adult stage were approximately 10% greater in the highlands than lowlands. This observed difference highlights the importance of the adult stage for Red-tailed Hawk populations in the dynamic environment of the highland forests of eastern Puerto Rico.

There is a positive relationship between adult survival and body mass in diurnal birds of prey (Newton *et al.* 2016). Continental *Buteo* hawks with similar body mass as the Red-tailed Hawk in Puerto Rico have exhibited survival rates of 70 – 88% (Preston & Beane 1993, Kenward *et al.* 2000, Schmutz *et al.* 2006, Schmutz *et al.* 2008). However, species of island raptors exhibit greater rates of adult survival than continental forms (Gliwicz 1980, Adler & Levins 1994, Stutchbury & Morton 2001). Adult survival rate of the Red-tailed Hawk in Puerto Rico (≥ 95%) was similar to other species of mainland Neotropics and island raptors, including Barred Forest Falcon *Micrastur ruficollis* (95.3%), Hawaiian Hawk (94%), Ridgway's Hawk *Buteo ridgwayi* (94%) and the Galapagos Hawk *Buteo galapagoensis* (94%) (Klavitter *et al.* 2003, Nimitz 2005, Rivera-Parra *et al.* 2012, Thorstrom 2012, The Peregrine Fund unpubl. data).

Greater rate of annual survival may be linked to lifespan, a trait observed in tropical and island species as well as several raptor species (Snow & Lill 1974, Grant & Grant 1992, Stutchbury & Morton 2001, Klavitter *et al.* 2003, Krüger 2007, Newton 2016). Based on our results, we suggest annual survival of adult Red-tailed Hawks and lifespan may have a greater influence on population growth compared to reproductive success, a pattern previously reported for other raptor species (Sæther & Bakke 2000, Sæther *et al.* 2004, Katzner *et al.* 2006, Krüger 2007, Krüger*et al.* 2010). Our seasonal matrix model results suggested greater adult and juvenile survival were important components sustaining population growth of the Red-tailed Hawk in the highlands of eastern Puerto Rico, despite scenarios of relatively low reproductive success (nestling and fledgling) as reported by Santana and Temple (1998).

Several raptor species in the mainland tropics and islands exhibit reduced clutch size, either by producing smaller clutches or not breeding every year (Donázar 1990, Simmons 2000, Evans *et al.* 2005). While some species of tropical and insular raptors have smaller clutch sizes, average clutch size (2.3 eggs) of the Red-tailed Hawk in eastern Puerto Rico was similar to mainland populations in other parts of the geographic range where average clutch size ranges from 2.11 to 2.94 eggs (Santana & Temple 1988, Preston & Beane 1993, Clarkson & Laniawe 2000, Woolaver *et al.* 2014, de Vries 2015). These results suggest clutch size of the Red-tailed hawk in eastern Puerto Rico may partially explain population growth rates despite lesser nestling success (e.g. highlands = 30%). The Red-tailed Hawk in Puerto Rico produced a proportionally greater number of fledglings/female (lowlands = 1.7 and highlands = 0.7) than other threatened and end endangered raptor species of the region (Puerto Rican Sharp-shinned Hawk = 0.38, Ridgway's Hawk = 0.8) per nesting attempt (Delannoy & Cruz 1988, Santana & Temple 1988, Thorstrom *et al.* 2005). The combination of adult and juvenile annual survival and greater number of fledglings may explain the greater sensitivity value of nestling survival on the third transition time in the lowlands (0.46) and highlands (0.48), highlighting the importance of this stage in the estimated value of λ for the Red-tailed Hawk in eastern Puerto Rico.

Our results suggest that the population of Red-tailed Hawks in eastern Puerto Rico exhibited traits typical of species in the initial phases of island colonization. These are characterized by the early phase of logarithmic population growth driven by high adult survival and reproductive success (MacArthur & Wilson 1967). The long-distance migratory capabilities of the Red-tailed Hawk may have played an important role in the ability of this common continental species to colonize most islands of the Greater Antilles (Raffaele *et al.* 1998). Furthermore, demographic traits of this species may have further facilitated the process of island colonization. In Eurasia, the Common Buzzard *Buteo buteo* has comparable ecological requirements to the Red-tailed Hawk, including long-distance migratory populations and insular subspecies (Ferguson-Lees & Christie 2001, Bildstein 2006, Hardey 2006). Rodríguez *et al.* (2010) reported insular subspecies of the Common Buzzard *Buteo b. insularum* on the island of Tenerife retain reproductive values similar to the nearest mainland populations but utilize a wider range of nesting habitats compared to continental populations.

By retaining some mainland traits (e.g. clutch size) and traits typical of tropical islands (e.g. high annual survival) the Red-tailed Hawk in eastern Puerto Rico exhibited sustained population growth in the highlands ($\lambda = 1.05$, $r = +0.05$) and lowlands ($\lambda = 1.27$, $r = +0.24$). However, other factors not accounted for by our model may also influence populations (e.g. differences in gender mortality) of the Red-tailed Hawk in eastern Puerto Rico. Nevertheless, the traits mentioned may partly explain the documented greater densities of Red-tailed Hawks and degree of territory overlap in the highlands of the Luquillo Mountains (Boal *et al.* 2003, Nimitz 2005, Vilella & Nimitz 2012). We propose two behavioral non-mutually exclusive hypotheses to partially explain our observed lesser values of λ in the highlands based on the Red-tailed Hawk traits mentioned. These include the individual adjustment hypothesis and the habitat heterogeneity hypothesis. The former argues the documented greater abundance and spatial overlap might result in increased agonistic interactions among neighboring Red-tailed Hawks, resulting in individuals displaced to areas of reduced habitat quality, with a consequent reduction in overall breeding success and reduced population growth in a specific area (Ferrer & Donazar 1996). The latter would address the establishment of a hierarchy, whereby the use of low quality territories would result in reduced breeding success (Rodenhouse *et al.* 1997). Therefore, we suggest the highlands of the Luquillo Mountains may represent low-quality breeding habitat given the influence of extended periods of severe weather (e.g. rain and fog) on nesting success and the consequent negative impact on local population growth.

Matrix algebra has been widely used to describe the dynamics of wild populations, including raptors (Klavitter *et al.* 2003, Krüger 2007). However, the most widely used approaches (e.g. Leslie matrix) are not designed to account for the contribution of early life stages to population growth. Seasonal matrix models can be a useful tool to explore the importance of early life stages (e.g. nest success) on the dynamics of insular populations. Further, seasonal models may be useful to describe the potential effect on population growth of density-independent and density-dependent processes by identifying early life stages that may require conservation management measures (Caswell 2001, Davis *et al.* 2004, Westernman *et al.* 2005, Bacaër 2007, Jenouvrier *et al.* 2010,Caswell& Shyu 2012). Our approach can be applied to other non-migratory species to identify vulnerable life stages that may require conservations and management actions and evaluate their efficiency (Flockhart *et al.* 2015, Hostetler *et al.* 2015). This modeling approach can be adapted to other island raptors with alternative breeding strategies such as the polyandrous Galapagos Hawk or the Hawaiian Hawk, a species that breeds on alternate years and lays a single egg per breeding attempt. For these island raptors, early life stages may play a major role in their population dynamics that may be overlooked using other population modeling approaches (Clarkson & Laniawe 2000, Hostetler *et al.* 2015).

Our results suggested lowland habitats characterized by isolated woodlands separated by grasslands, early sucessional forest, and urban development may promote population growth of Red-tailed Hawks in eastern Puerto Rico. Disturbance events such as major hurricanes increase forest openings, benefitting foraging success of Red-tailed Hawks while increasing the exposure avian species dependent on closed canopy forest like the Puerto Rican Parrot, to predation (Snyder *et al.* 1987, Brokaw & Walker 1991, Beissinger *et al.* 2008). Hurricane Maria made landfall in eastern Puerto Rico on 20 September 2017 with sustained winds of 250 km/hr. Damage to the forests of the Luquillo Mountains was extensive and hurricane impact on resident wildlife, including the Red-tailed Hawk, has not been assessed. Abundance patterns and population growth rate of Red-tailed Hawks in eastern Puerto Rico together with forest habitat impacts from Hurricane Maria may limit recovery efforts for the Puerto Rican Parrot, at least during the initial years following this major storm (Snyder *et al.* 1987, White *et al.* 2005). Vital rates of Caribbean Red-tailed Hawks should be updated to better understand post-hurricane effects (positive or negative) on the population dynamics of this top predator of the Caribbean islands.

Table 4.1 Life-stage survival probabilities values of Caribbean Red-tailed Hawk (*Buteo j. jamaicensis*) in Puerto Rico.

Life-stage parameter/ Survival probability	**Value**	**Reference**
Adult (A), adult survival (S4)	0.97	Nimitz 2005
Juvenile survival (J), second-year survival (S5)	0.95	Nimitz 2005
Clutch survival (C), highlands ($S1_h$)	0.6	Santana and Temple 1988
Clutch survival (C), lowlands ($S1_l$)	0.78	Santana and Temple 1988
Nestling survival (N), in highlands ($S2_h$)	0.7	Santana and Temple 1988
Nestling survival (N), in highlands ($S2_l$)	1.5	Santana and Temple 1988
Fledgling survival (F), in highlands ($S3_h$)	0.3	Santana and Temple 1988
Fledgling survival (F), in lowlands ($S3_l$)	0.65	Santana and Temple 1988
Fecundity (Fc)	1.15	Santana and Temple 1988

Table 4.2 Sensitivity and elasticity matrices of λ to changes in values of each of the different time matrices of Red-tailed Hawk in of eastern Puerto Rico.

Time	**Sensitivity**	**Sensitivity**	**Elasticity**	**Elasticity**
	Upper forest	**Lowland forest**	**Upper forest**	**Lowland forest**
Transition 1	$\begin{pmatrix} 0.02 & 0.12^b \\ 0.15^a & 0.78^c \end{pmatrix}$	$\begin{pmatrix} 0.11 & 0.26^b \\ 0.31^a & 0.70^c \end{pmatrix}$	$\begin{pmatrix} 0.00 & 0.14^b \\ 0.14^a & 0.73^c \end{pmatrix}$	$\begin{pmatrix} 0.00 & 0.23^b \\ 0.23^a & 0.53^c \end{pmatrix}$
Transition 2	$\begin{pmatrix} 0.24^d & 0.24 \\ 0.93 & 0.93^c \end{pmatrix}$	$\begin{pmatrix} 0.38^d & 0.46 \\ 0.83 & 1.01^c \end{pmatrix}$	$\begin{pmatrix} 0.14^d & 0.00 \\ 0.00 & 0.86^c \end{pmatrix}$	$\begin{pmatrix} 0.23^d & 0.00 \\ 0.00 & 0.77^c \end{pmatrix}$
Transition 3	$\begin{pmatrix} 0.48^e & 0.77 \\ 0.58 & 0.94^c \end{pmatrix}$	$\begin{pmatrix} 0.46^e & 0.69 \\ 0.67 & 1.01^c \end{pmatrix}$	$\begin{pmatrix} 0.14^e & 0.00 \\ 0.00 & 0.86^c \end{pmatrix}$	$\begin{pmatrix} 0.23^e & 0.00 \\ 0.00 & 0.77^c \end{pmatrix}$
Transition 4	$\begin{pmatrix} 0.15^f & 0.79 \\ 0.18 & 0.94^c \end{pmatrix}$	$\begin{pmatrix} 0.31^f & 0.70 \\ 0.45 & 1.01^c \end{pmatrix}$	$\begin{pmatrix} 0.14^f & 0.00 \\ 0.00 & 0.86^c \end{pmatrix}$	$\begin{pmatrix} 0.23^f & 0.00 \\ 0.00 & 0.77^c \end{pmatrix}$

Transition 1: transition of juveniles to second-year birds ($S5^a$) and a breeding period that included, clutch size (Cl^b) adult survival ($S4^c$); Transition 2: transition through the incubation period and clutch survival ($S1^d$) adult survival ($S4^c$); Transition 3: transition through the nestling stage nestling survival ($S2^e$) adult survival ($S4^c$); and Transition 4: transition from fledging to juvenile (first-year, $S3^f$) adult survival ($S4^c$).

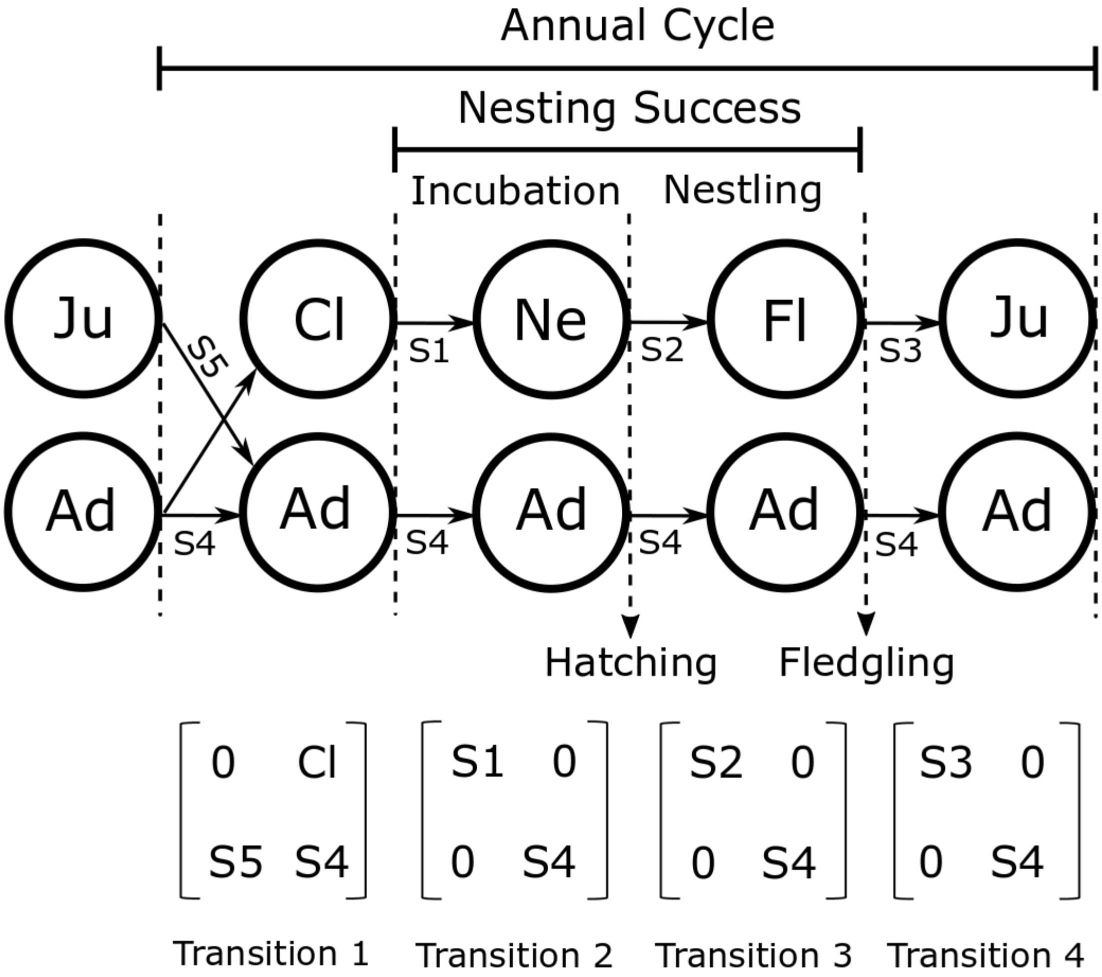

Figure 4.1 Annual cycle graph and projection transition matrices of the Red-tailed Hawk in eastern Puerto Rico. Fertility (Fc = 1.15) represented by the clutch stage and four life stages, 1) juvenile (J), adults (A), nestling (N), and fledgling (F). Matrices with corresponding survival probability include, clutch survival in the highlands (S1 = 0.60), clutch survival in the lowlands (S1 = 0.78), nestling survival in the highlands (S2 = 0.30), nestling survival in the lowlands (S2 = 0.60), fledgling/juvenile to one year old (S3 = 0.95), adult survival (S4 = 0.97), and second year bird survival (S5 = 0.97), and T each independent transitions matrices.

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CHAPTER V

RED-TAILED HAWK ABUNDANCE ESTIMATES AND HABITAT ASSOCIATIONS IN PUERTO RICO

Introduction

Describing how environmental conditions affect species-habitat relationships is essential to understanding species distributions (Brown 1984, Caughley 1994, Morrison et al. 2006, Jones 2001). Along with density-dependent factors, temporal and spatial differences in environmental conditions, habitats, and resources determine the abundance and distribution of animals (Dunning et al. 1992, Cody 1985, Newton 1998, Morris 2006, Krüger et al. 2012). Organisms may populate lower-quality habitats when abundance exceeds the capacity of preferred habitats. This is related to population density in that individuals may be more abundant at sites that meet all their life history requirements and only occupy other locations as resource levels vary (Fretwell and Lucas 1970, Krüger 2002, Boyce et al. 2016). An ecological niche can be defined as the sum of traits allowing individuals of a species to persist in a given area (Harte 2011, Peterson et al 2011). Geographic range, population dynamics, and niche can be reliable predictors of local abundance (Brown 1984, Brown 1995, Pulliam 2000, Harte 2011).

Organisms on oceanic islands exhibit unique resource use, including habitat and resource use expansion or shifts because of release from interspecific competition (Abbott 1980, Baker-Gabb 1986, Grant and Grant 2006). For some island species, this ecological release results in greater abundance and a wider range of habitats used compared to their mainland counterparts, a phenomenon described as density compensation (Crowell 1962, MacArthur et al. 1972, Blondel 2000). Common characteristics of island populations include greater adult and juvenile survival rates, reduced dispersion, lower productivity, longer breeding periods, and greater densities that lead to smaller home ranges (Gliwicz 1980, Adler and Levins 1994). On tropical islands, greater densities and increased survival, as well as intraspecific competition, may result in spillover of subordinate individuals (i.e., juveniles) into less suitable habitats (MacArthur et al. 1972, Blondel 2000). Habitat heterogeneity may play an important role in species distribution when resources are unevenly distributed throughout tropical island landscapes.

The Red-tailed Hawk (*Buteo jamaicensis*) is the most common and widespread raptor of the genus *Buteo* in North America, inhabiting a variety of open habitats with scattered perches (Preston and Beane 1993). In Puerto Rico, the Caribbean Red-tailed Hawk (*B. j. jamaicensis*; hereafter, RTHA) is a common diurnal raptor and coexists with six other resident raptors, including two endangered species: the Puerto Rican Broad-winged Hawk (*Buteo platypterus brunnescens*) and the Puerto Rican Sharp-shinned Hawk (*Acicpiter striatus venator*). Other raptor species in the eastern Caribbean region of Puerto Rico and the Virgin Islands include the Turkey Vulture (*Cathartes aura*), American Kestrel (*Falco sparverius*), Puerto Rican Screech-Owl (*Megascop nudipes*), and Short-eared Owl (*Asio flammeus*) (Raffaele 1992).

Contrary to continental populations that nest in open areas and generally avoid the forest interior, the RTHA in Puerto Rico nest across all elevations, including closed canopy montane forest. Nevertheless, the RTHA in Puerto Rico favor open woodlands and roadside habitats and areas in landscapes characterized by high patch and edge density (Santana et al. 1986, Santana and Temple 1988, Nimitz 2005, Vilella and Nimitz 2012). The greater reported concentrations of the RTHA in Puerto Rico are on the eastern portion of the island (Santana and Temple 1988, Boal et al. 2003, Nimitz 2005).

Birds of prey on oceanic islands play a major role in terrestrial food webs given the general absence of native mammalian predators (Losos and Ricklef 2009, Vilella and Nimitz 2012). Factors that drive abundance and habitat use of tropical raptors are still poorly studied and understood, especially for oceanic islands (Hall et al. 1997, Bildstein et al. 1998, Virani and Watson 1998, Klavitter et al. 2003, Piana and Marsden 2012, Rivera-Parra et al. 2012, Whitacre and Burnham 2012). Spatial and temporal variation in environmental conditions and resource distributions can affect the arrangement of individuals in the landscape (i.e., territoriality), consequently influencing abundance (Brown 1995, Newton 1998, Newton 2013, Boyce et al. 2016, Kéry and Royle 2016). Unreliable estimates of animal abundance can lead to erroneous inferences on population status, limiting the capacity for conservation and management (Farnsworth et al. 2002, Sillett et al. 2012, Amundson et al. 2014). Attempts to estimate animal abundance should account for spatial variation in animal density (Farnsworth et al. 2002).

Regardless of the target species, estimating abundance should address two measurement errors that can introduce bias estimates: 1) underestimates resulting from failing to detect an individual (imperfect detection) and 2) overestimation as a result of counting the same individual multiple times (Dénes et al. 2015, Kéry and Royle 2016). Imperfect detection (false absence) and its sources of variation can be a potential basis for abundance estimates and any inferences about habitat use, having implications for assessments at individual, survey, species, and community levels (Buckland et al. 2001, MacKenzie 2006, Dénes et al. 2015). Different factors, such as the observer, time of day, weather, survey methods, survey site, species traits (i.e., conspicuousness, behavior, life history, and rarity), and individual differences (Iknayan et al. 2014), can influence variation in detection. However, the probability of detecting an organism is conditioned by its presence at a given site (occupancy), availability (given presence), and detectability (given presence and availability) during a sampling period (Pollock et al 2004, Nichols et al. 2009, Chandler et al. 2011, Tozer et al. 2016). Certain habitats and behavioral traits of species and individuals (i.e., overlapping territories, highly mobile species, variations in breeding phenology) may influence the number of individuals available to be detected at a survey plot (Pollock et al 2004, Chandler et al. 2011). A demographically open survey point may lead to an overestimation of individuals (super populations) or temporary absences (nonpermanent occupied sites), both resulting in biased abundance estimates (Pollock et al 2004, Chandler et al. 2011, Kéry and Schaub 2012, Dénes et al. 2015, Kéry and Royle 2016). In Puerto Rico, the RTHA shows several island traits that may be sources of bias when estimating habitat associations, such as high mobility and territory overlap (Boal et al. 2003, Vilella and Nimitz 2012).

I conducted road surveys in the Luquillo Mountains and Cordillera Central to 1) estimate the RTHA populations in the Luquillo Mountains and Cordillera Central and 2) develop landscape habitat models to identify variables contributing to RTHA abundance. I developed empirically based models to estimate RTHA abundance (N_{it}), the probability of presence during a sampling period (ϕ), and detection probability (r) with the goal of understanding the relationships between these parameters, taking into consideration site and survey variables. The intended outcome of this study was to provide accurate estimates of the abundance of a native and widespread predator on an oceanic tropical island.

Methods

Study area

The areas selected for this study were the Luquillo Mountains and the Cordillera Central in Puerto Rico. Located on the northeastern side of the island, the Luquillo Mountains represent the region with the most complex physiographic features, encompassing five of the six life zones described for Puerto Rico (Ewel and Whitmore 1973). This mountain range is the main formation in northeast Puerto Rico, with an elevation ranging from 200 m to 1,080 m and a mean annual precipitation of 200–500 cm. The Luquillo Mountains include the largest remaining tracts of primary montane forest (El Yunque National Forest) on the island (Ewel and Whitmore 1973, Lugo 1994, Foster et al. 1999). Currently, urban development in the Luquillo Mountains is happening at one of the highest rates on the island, where a growing urban sprawl and its related effects are increasing the fragmentation and isolation of El Yunque Forest (Páres-Ramos et al. 2008, Castro-Prieto et al. 2017).

The Cordillera Central is characterized by rough terrain and steep slopes with elevations reaching 1,338 m. Average rainfall ranges from 234 cm to 4,000 cm, with most rainfall occurring on the eastern side of the mountains (Delannoy 1984, Delannoy 1997, Fogarty and Vilella 2002). The Cordillera Central encompasses three of the six ecological life zones of Puerto Rico: subtropical lowland moist forest located in the lower parts and up to 400 m, subtropical wet forest at elevations from 400 to 700 m, and subtropical lower montane wet forest above 700 m (Ewel and Whitmore 1973). The major sources of landscape change in the Cordillera Central are increasing housing development in rural areas and forest regeneration in abandoned agricultural plots and pastures (Marcano-Vega et al. 2002, Castro-Prieto 2017). The southwestern region of Puerto Rico is constituted of a mosaic of active and abandoned agriculture land, pastures, grasslands, and deciduous and semideciduous forest (Gould et al. 2008).

Field Procedures

In Puerto Rico, the RTHA is found in all habitats and at all elevations, and its abundance is one of the highest recorded along the species' distribution (Nimitz 2005, Llerandi 2006). It has been proposed that such high abundance is influenced by landscape features such as steep slope and that their abundance decreases with elevation (Rivera-Milán 1995, Boal et al. 2003). To assess the effect of landscape variables on the abundance of the RTHA in Puerto Rico, I developed abundance estimates and habitat associations, namely mean slope and elevation. Additionally, I modeled factors that might influence detection such as visual obstruction (forest canopy closure), wind speed, and time of day where the survey was conducted, which might affect the flying activity of the RTHA (Kerlinger 1989, Johnson 2007). I conducted fixed-radius point-transect surveys along primary and secondary roads in the Luquillo Mountains and Cordillera Central (Figure 5.1). In the Luquillo Mountains, I established 19 routes (127 points) and on the western side of the Cordillera Central (in Maricao Forest and adjacent areas), I established 13 routes (91 points). Each survey point was surveyed 6 times with at least 15 days between each survey at that point, during the RTHA's breeding season (i.e., mid-November to mid-July). Survey routes were composed by 5 to 7 survey points spaced by an odometer distance of 1.6 km (Nimitz 2005). I sampled survey points systematically in numerical order until the route was done; maintaining a constant speed of 25 km/hr moving between stations (Fischer et al. 1984, Rivera-Milán 1995, Nimitz 2005, Llerandi 2006).

Detection of individual hawks might be influenced partially by distance from the observer and visual obstruction (Buckland et al. 2001). Previous research in Puerto Rico indicated RTHA detection probability decreased at distances of800–1,000 m from the point center of a survey plot without visual obstruction (i.e., canopy platforms) (Nimitz 2005). However, my survey points along roads were in a wide range of habitats and elevations that are associated with a variety of visual obstructions. On the other hand, the accuracy of estimates is linked to the precision of the measured distance while including individuals in a count (Buckland et al. 2001). I tested the accuracy of two laser rangefinder models: the Nikon Prostaff 7i (Nikon Corporation) with a maximum distance of 500 m (n = 100, mean = 493.62 m, SE = 0.45) and the Bushnell Yardage Pro 1000 (Bushnell Corporation) with a maximum distance of 1,200 m (n = 100, mean = 1055.27 m, SE = 0.81).Therefore, to reduce bias in detection caused by distance and visual obstruction, I used 500 m from the point center as the cutoff distance for counts and as a buffer radius for the development of spatial variables.

Surveys were conducted on clear to mostly sunny days each month until all survey points of a started route were completed (Llerandi 2006). To reduce bias in estimates of local abundance caused by a surplus of non-territorial individuals (potentially more mobile) or by counting the same individual multiple times, I only included in the analysis flying second-year and adult RTHAs (individuals with an orange-red tail) found within a 5-minute survey period (Preston and Beane 1993, Ferguson-Lees and Christie 2001, Nimitz 2005). All survey times were conducted in a period between 730 and 1630 hrs, which is the period when RTHA are most actively flying (Santana and Temple 1988, Llerandi 2006). Additionally, I recorded wind speed measures (km/hr) with a Kestrel® 4500 Pocket Weather Tracker Monitor (Nielsen-Kellerman, Boothwyn, PA) one-minute lecture before and after (later averaged) every count at every survey point.

Database development and abundance estimates

To estimate the abundance of the RTHA throughout my study area and its relationship with features of the landscapes, I included elevation at survey point, average canopy closure, and mean slope as site-specific variables. For every survey point, I created a 500m buffer in ArcMap (ESRI 2006) to extract values of each spatial variable. Elevation at each point was obtained from the Puerto Rico Digital Elevation Model (DEM),with a resolution of 30 m (NOAA 2012). I created a slope digital model based on the Digital Elevation Model of Puerto Rico (NOAA 2012; 30 m resolution) and extracted mean slope values of each point using the Spatial Analyst extension in ArcMap (ESRI 2006). I used a model developed for Puerto Rico (Huang et al. 2004; 30 m resolution) to estimate percentage of forest canopy closure using a vector zonal statistic approach in ERDAS Imagine 13.0 (ERDAS Imagine Geospatial Imaging 2009). I included survey-specific variables that might affect the activity of the RTHA, namely wind speed and survey time (Johnson 2007). Survey starting time was standardized by minutes after sunrise (Astronomical Applications Department of the United States Naval Observatory 2015) for each location: Mayaguez (2012 and 2013) and San Juan (2012 and 2013).I tested potential multi-collinearity of site-specific and survey-specific variables by performing a variance inflation factor (hereafter, VIF) analysis using the VIF function (package usdm in program R; Naimi 2015) as suggested by Zurr et al. (2007). I only included variables with values of ≤5, as recommended in other spatial modeling studies of birds of prey (Montgomery and Peck 1992, Zurr et al. 2009b, Sarà 2014).

Landscape heterogeneity may in turn induce heterogeneity in the detection estimates due to net detection probability being tightly related to the number of individuals available at a specific site (Pollock, et al. 2004, Dénes et al. 2015). I applied a generalized binomial n-mixture model for counts of unmarked individuals in repeated time (t) and space (i) using package unmarked (program R; Fiske et al. 2015). I used negative binomial and/or Poisson distributions to evaluate the effect of plot-specific covariates (elevation, canopy closure, and slope) to estimate the number of RTHAs around the survey plot (N_{it}), and I used primary survey periods to test for differences in availability of individuals (ϕ). I used survey-specific covariates (survey time and wind speed) and a plot-specific covariate (canopy closure) to model mean individual detection probability (r; hereafter*,* detection probability), which is the probability to detect each individual in a survey plot (Chandler et al. 2011, Kéry and Royle 2016). To account for potential differences in availability of RTHAs during counts due to the partial absence of individuals during incubation, I split the surveys into two different primary counts with three secondary visits each (nested). The first primary period was from November to

March, which comprised the beginning of the breeding season and included the peak of egg laying, where potentially one individual of a pair is incubating and unavailable for counts (Santana and Temple 1988). The second period was from April to July, comprising the nesting stage and the peak of fledging, where both individuals of a pair are outside of the nest and potentially available to be counted during surveys (Santana and Temple 1988).

I created a set of competing models by building models with each of the single covariates to explore linear relationships, then models with the quadratic effect of covariates, and finally models containing biologically important covariate combinations and interactions. I tested for potential differences in the number of RTHAs available to be counted during the survey periods by including both survey periods as a categorical variable of availability in the model. I ranked models based on Akaike's Information Criterion values corrected for small sample sizes (AICc). To compare with previous RTHA estimates in the Luquillo Mountains (Nimitz 2005), I presented the model estimates without variables (null model) and used the back-transform function in package unmarked in R to rescale log values to original-scale values. I considered ΔAICc ≤ 2 as competing models (Burnham and Anderson 2002). To evaluate data distribution fit, I selected the model with the smallest ΔAICc value and changed the family from a Poisson error distribution to a negative binomial. I then ran the model selection again to compare their respective values of overdispersion (greater variance than expected as function of covariates; $\hat{c}$); when $\hat{c} \sim 1$, this indicated a good fit of the data with a specific distribution and accurate abundance estimates (Kéry and Royle 2016).

All models were fitted using function gpcount in package unmarked in R (Chandler et al. 2011, Fiske et al. 2015). I used parametric bootstrapping with 1,000 simulations to test overall model fit using the Nmix.gof. test function of the package AICmodavg in Program R, where *P* values > 0.05 indicate adequate fit, under the null hypothesis that states no differences between the collected data and the simulation data (Fiske et al. 2015, Kéry and Royle 2016). In addition, I selected a group of survey points separated by a linear distance of 2,700 m, which is the diameter of the average core territory of RTHA in Luquillo Mountains (Vilella and Nimitz 2012), then I compared the estimates. I produced a map of the residuals (averaged over survey sessions) to investigate spatial structure of the best competing model using function map.Nmix.resi in package AHMbook and the gstat package to plot averaged residuals over replicated surveys (Kéry and Royle 2016). All covariate values were z-transformed prior to the analysis to facilitate estimate comparisons between covariates and model convergence (Kéryand Chandler 2012, Tozer et al. 2016). Finally, I plotted abundance and detection estimates as a function of significant covariates ($P \leq 0.05$) of the best competing model to explore relationships.

Results

All the selected variables used to model abundance and detection in the Luquillo Mountains and Cordillera Central showed a non significant autocorrelation with VIF values < 3.5 (Table 5.1). At least one RTHA was recorded in the Luquillo Mountains on 123 of 127 survey points, with 754 RTHA sightings. The average of RTHAs detected per survey point was 0.99 (SE= 0.043, range= 0–6), ranging from 0.83 to 1.15 per survey session (Figure 5.2). Surveys in the Luquillo Mountains were conducted during days with average wind speed of 5 km/hr (range = 0–24.3 km/hr), at an elevation averaging 239.94 m (range = 7.89–1055.52 m), and the mean slope was 12.18˚ (range = 0.68–24.81˚). In the western Cordillera Central, at least one RTHA was recorded in all 91 survey points, with 609 sightings. The average of RTHAs detected per survey point was 1.115 (SE = 0.053, range = 0–6) ranging from 0.69 to 1.49 per repetition (Figure 5.3). Surveys in the western Cordillera Central were conducted under average wind speed of 4.078 km/hr (range = 0–30 km/hr), elevation averaged 324.11 m (range = 54.54–896.07 m), and slope averaged 17.42˚ (range = 6.49–27.58˚).

In Luquillo Mountains, the null model gave estimates of 3.93 RTHA (SE = 0.213) per survey point (0.05 RTHA/ha), an availability of RTHA of $(\phi) = 0.998$ (SE = 0.009) per survey point, and a detection probability $(r) = 0.252$ (SE = 0.011).In the western Cordillera Central, the null model gave estimates of 4.09 RTHA (SE = 0.250) per survey point (0.05 RTHA/ha), an availability of RTHA of $(\phi) = 1$ (SE = 0.005) per survey point, and a detection probability $(r) = 0.273$ (SE = 0.013).The null model for Luquillo Mountains (29 survey points) gave estimates of 4.02 RTHA per survey point (SE = 0.46), an availability of RTHA of $\phi = 1$ (SE = 0.01) per survey point, and a detection probability $(p) = 2.2$ (SE = 0.02). The null model of western Cordillera Central (25 survey points) the null model gave estimates of 4.02 RTHA (SE = 0.47) per survey point (0.05 RTHA/ha), an availability of RTHA of $\phi = 1$ (SE = 0.01) per survey point, and a detection probability$(r) = 2.8$ (SE = 0.02).

In the Luquillo Mountains, the ΔAICc values ranged from 0.0 to 23.62, but only four competing models had a $\Delta\text{AIC}_c \leq 2$ (Table 5.2). The variables represented in the four best competing models included mean canopy closure, mean slope, a quadratic effect of elevation on abundance (N_{it}), and survey time for detection probability (r). Variables with $P < 0.05$ in at least one competing model with a $\Delta AIC_c \leq 2$ showed that mean slope and quadratic effect of elevation for abundance and survey time and mean canopy closure for detection had similar effect in all models.

Comparing the most parsimonious model using Poisson distribution (model 5) and the negative binomial (model 6) distributions, I found the latter exhibited the better fit for the RTHA count data in the Luquillo Mountains ($\hat{c} = 1.29$, $P = 0.11$). The composition of model 3 showed variables with a significant effect ($P < 0.05$) that did not contain zero in their 95% confidence intervals are mean slope and quadratic effect of elevation for abundance, and canopy closure and survey time for detection (Table 5.3).

In the western Cordillera Central, values of ΔAICc ranged from 0.0 to 40.48, however only two competing models exhibited $\Delta AIC_c \leq 2$. Both competing models contained the same variables in their structure, one with Poisson distribution and the other with negative binomial distributions (Table 5.4). No variables were present in the ecological part of model (abundance, N_{it}); wind speed, survey time, and interaction of wind speed and mean slope were present in detection probability (r), and primary survey periods were present in availability (ϕ). When I compared both models, the negative binomial distribution showed a better fit for the RTHA count data in the Cordillera Central ($\hat{c} = 1.29$, $P = 0.11$). The interaction of wind speed and mean slope had a significant negative effect on detection probability ($P > 0.05$).

Map of residuals (averaged over replicate surveys) of the model with lowest ΔAICc for the western side of Cordillera Central and the Luquillo Mountains with negative binomial structure exhibit local pockets of high or low values in its spatial structure (Figure 5.4 and Figure 5.5).

Discussion

Previous studies suggested the greatest reported abundances (e.g., 0.01 RTHA/ha in the Luquillo Mountains) for the RTHA throughout their geographic range were found in Puerto Rico (Nimitz 2005, Llerandi 2006). However, my results suggest abundance may be even greater than these previous reports (i.e., up to five times) and may be partially influenced by landscape features in the Luquillo Mountains such as steep slopes and elevation. For example, greater slope values (> 20˚) along my survey routes predicted up to 6 RTHA per point (Figure 5.6). Previous research suggested hilltops and ridgelines represented geographic features favorable for foraging, soaring and territory defense as RTHA exploit the updrafts generated by the easterly trade winds in the Luquillo Mountains (Snyder et al. 1987, Boal et al. 2003, Nimitz 2005). The strength of these updrafts decreases with slope, which can be negatively correlated with lower concentrations of flying hawks in areas with lesser slope values, such as the lowlands surrounding the Luquillo Mountains (Kerlinger 1989). This phenomenon has been observed in other soaring raptors such as the Black-chested Eagle-buzzard (*Geranoaetus melanoleucus*), the adults of which concentrate in steep slopes where wind conditions favors a more economical flight to hunt and patrol territories (Bustamante et al. 1997). Therefore, my results suggest that the RTHA concentrates in areas with steep slopes in the Luquillo Mountains, thus increasing local abundance.

My results indicated a nonlinear relationship between abundance and elevation where RTHA numbers were greater at elevations between 200 and 400 m in the Luquillo Mountains (Figure 5.7). This result differs from Nimitz (2005), who reported no differences in RTHA abundances between subtropical moist (0 to 400 m) and subtropical wet (400 to 700 m) life zones. However, Nimitz did not account for landscape variables while estimating abundance. On the other hand, my results support the findings of Rivera-Milán (1995), who found that RTHA abundance decreased with elevation, however, he estimated relative abundance and did not account for imperfect detection. Judging for the confidence interval lines of Figure 5.7, the predictions may not be biologically significant while comparing the number of RTHAs in the elevational gradient, but it may suggest a distribution pattern of where RTHAs are concentrating. Kerlinger (1989) suggests that the strength of the updrafts is stronger at the foothills of a mountain, where trade winds experience the first resistance when hitting the slopes in the first couple of hundred meters of elevation. This suggests that the eastern and southeastern sides of the Luquillo Mountains had the steepest slopes in the first 200 to 600 m of elevation, potentially offering good flying conditions for the RTHA to concentrate.

At the habitat level, the structure and composition of forest habitats in the Luquillo Mountains may play an important role in RTHA abundance. The RTHA in Puerto Rico nest in emergent trees with an average height ranging from 12.3 m to 18.4 m in the lowlands (0–400 m) and 19.8 m to 26.6 m at upper elevations above 400 m (Santana et al. 1986). Brown et al. (1983) reported a general pattern in composition and structure of forests in the Luquillo Mountains, where species diversity, tree height, diameter, and basal area of trees decrease as elevation increases, with the possible effect of limiting the number of suitable nesting sites and consequently, reducing the abundance of RTHA at higher elevations. Similarly, the Hawaiian Hawk (*Buteo solitarius*) is common and widespread in most of the island of Hawaii and it is rarely found at higher elevations (Clarkson and Laniawe 2000). Klavitter et al. (2003), found the greatest density of Hawaiian Hawks in habitats characterized by a matrix of native forest with interleaved grasslands patches (0.92 hawks/km^2) and lesser abundances in shrubland, barren areas (e.g., lava fields), and urban areas (<0.19 hawks/km^2). On the other hand, is hypostatized that high abundance of prey such as pigeons and doves (Columbidae) and rodents contribute to the high abundance of RTHA in the Luquillo Mountains (Zwank and Layton 1989, Rivera-Milán 1992, Vilella and Nimitz 2012). I did not test for prey availability, but beyond prey abundance, my results suggest that some landscape configurations of the Luquillo Mountains may offer conditions for soaring that may facilitate economic soaring for hunting and increase hunting success, resulting in high local RTHA abundance.

My results suggest the abundance of the RTHA in the western side of the Cordillera Central is similar to the Luquillo Mountains. However, I found abundance of RTHA in the Cordillera Central was not associated with elevation, slope, or canopy closure. This suggests RTHA were potentially equally distributed across the landscape in the western Cordillera Central. The RTHA in Puerto Rico is associated with openings and roadside habitats in landscapes characterized by greater patch and edge density (Santana et al. 1986, Santana and Temple 1988, Llerandi 2006, Vilella and Nimitz 2012). In other regions of Puerto Rico, such as the northern karst and northwestern Cordillera Cental, Llerandi (2006) reported annual home range of the RTHA include forest patches and approximately 27% open habitats. The major source of landscape change in the Cordillera Central is small scale housing development in rural areas and increased forest cover from abandoned agriculture (e.g., coffee, cacao, and citrus plantations) and pastures (Marcano-Vega et al. 2002, Castro-Prieto 2017).The mosaic of forest fragments, active and abandoned agriculture, and other low scale agricultural areas of the Cordillera Central can be an important factor that favors high abundance of RTHA through the landscape.

In the Luquillo Mountains and west side of the Cordillera Central estimated availability was ~1 RTHA per survey site. In this case, availability values can be considered as a proxy of the number of territorial individuals, which is approximately 0.01 RTHA/ha, which is similar to previous abundance estimates (Nimitz 2005, Llerandi 2006). Spatial limitation (e.g., islands) and habitat saturation as result of high density may prevent some RTHA individuals from acquiring a territory (Penteriani et al. 2011).This may suggest that the RTHA abundance estimates here presented potentially include a surplus of non-breeding individuals (floaters) and/or nonlocal breeders that move throughout the area and form a super population. The non-breeding raptors tend to have a greater home range on average than breeding individuals, which may increase the number of individuals present in a given area (Bloom et al. 1993). Extensive spatial overlap in the Luquillo Mountains of RTHA territories, high abundance, and island population traits such as high annual survival (reported in previous studies; Boal et al. 2005, Nimitz 2005, Vilella and Nimitz 2012) can partially explain the presence of floaters that results in the higher abundance here reported. Vilella and Nimitz (2012) suggest that the Luquillo Mountains have some communal areas where RTHAs are concentrating with reduced agonistic behavior. This phenomenon may be favored by traits such as reduced aggression (experienced by some island populations) and potentially extended at least to the areas where individual territories meet. This can potentially be observed in other areas with high RTHA abundance, for example the west side of the Cordillera Central. Dispersing individuals and floaters are known to play an important role in the spatial-temporal distribution, trajectory, dynamic, and stability of animal populations (Penteriani et al. 2005, Penteriani and Delgado 2009, Penteriani et al. 2011). High presence of floaters may play an important role in explaining high abundance reported in this study and the stable territories suggested by Boal et al. (2003).

The detection probability of the RTHA in the Luquillo Mountains was influenced by two variables, survey (negative effect) time and canopy closure (positive effect). Generally, activity of individuals can affect detection probability, wherein encounter rates for diurnal birds are inversely proportional to time of day (Titus and Mosher 1981, Rollfinke et al. 1990, Tozer et al. 2017). The predicted RTHA detection probability in the Luquillo Mountains was greatest at 100 minutes (r = ~0.35) after sunrise (0900 hrs) and had decreased to r= 0.2 at by 1700 hrs (Figure 5.8). Time of day and season can influence raptor behavior and distribution (Iknayan et al. 2014). All RTHA sightings included in the analysis were detected during flight, which in this case may reflect that the probability of detecting an RTHA depends on individual behavior when engaging in foraging or territory-defense activities. In diurnal raptors these activities normally occur with greater frequency early in the day during0900–1100 hrs (Newton 1979). Detection probability in the Luquillo Mountains increased (0.22 to 0.28) with increasing canopy closure of 0 to 80% (Figure 5.9). The Luquillo Mountains are experiencing increased rates of urban development near protected areas (i.e., El Yunque National Forest), with consequently reduced forest cover and canopy closure associated with lower elevations (Castro-Prieto et al. 2017). The positive effect of canopy closure in detection probability can be a confounding outcome of high density of RTHAs attracted to forested areas. Newton (1986) found a positive correlation of forest cover with slope and suggested that steep slopes are a deterrent for human activities such as agriculture. Based on the findings of my study, as slope increases RTHA abundance also increases; therefore, RTHA abundance increases with canopy closure.

Detection probability of RTHA in the western Cordillera Central was negatively influenced by the interaction of slope and wind. Detection probability decreased with increasing slope and strong wind conditions. On the other hand, detection probability exhibited a gradual negative decrease with slope during gentler winds conditions (Figure 4.10). Surfaces with shallower slopes generally favor thermal formation (vertical ascendant warm winds) that helps soaring raptors (Kerlinger 1989). At lesser slope values, detection probability was greatest in regards to wind speed. However, at medium wind speeds (e.g., ~10 km/hr) detection probability can be greater than at slower wind speeds. Detection probability was greater in the Cordillera Central than the Luquillo Mountains, potentially because of the location of roadside survey points. The majority of the roads in the western Cordillera Central were located over ridge tops, offering better visibility than in the Luquillo Mountains, where several roads followed the contour of the mountains and located along forest patches and openings.

Road surveys may show some bias due the lack of randomization, but previous studies where surveys were conducted from canopy-level platforms in El Yunque National Forest (i.e., Luquillo Mountains) reported similar RTHA densities (Buckland et al. 2001, Nimitz 2005). However, roadside surveys allow sufficient effort to derive estimates of density and associated precision using empirical models of detectability (Ellis et al. 1990, Sorley and Andersen 1994, Buckland et al. 2001, Seavy and Apodaca2002, Jensen et al. 2005). The spatial autocorrelation found in some areas of my study sites may be partially explained by the non-random locations of roadside survey points and short linear distance of some points due to the topography of the mountains and location of the roads where surveys were conducted. Santana and Temple (1988) estimated an increase of 4 RTHA individuals during the non-breeding season representing the increment of first-year individuals into the population. My results present a snapshot of RTHA abundance during the breeding season prior to the surplus of juvenile individuals after fledglings, thus inferences made here are limited to that part of the population.

The ecology of the RTHA in Puerto Rico is probably the best known of all Neotropical populations of this widely distributed raptor (Santana et al. 1986, Santana and Temple 1988, Boal et al. 2003, Nimitz 2005, Llerandi 2006, Vilella and Nimitz 2012). However, knowledge of the mechanisms regulating their abundance limits our capacity to understand the ecological effects of this top predator on an island environment. Island traits such as high annual survival and a potentially increasing population growth (see Chapter IV) may suggest the presence of a surplus of RTHA individuals of the on the island. My results suggest that some traits of the RTHA play an important role in sustaining a great population of floater individuals that may influence the species population and spatial dynamics and explain a high abundance in Puerto Rico. Understanding the dynamic of this super population composed by non-breeding individuals is crucial to understanding population dynamics that support high abundance of the RTHA in Puerto Rico. Beyond high abundance, a high prevalence of a surplus of non-breeding RTHAs in Puerto Rico may explain a persistence of territories over time, as suggested by Boal et al. (2003), by allowing a high individual replacement rate when a territory vacancy occurs.

Further research about the role of floaters on the population dynamic of the RTHA in Puerto Rico is needed to understand the full extent of the impact high abundance of this top predator has on the animal populations that it preys on. An abundant predator such as the RTHA can have a greater impact on endangered species with small populations, such as the Puerto Rican Parrot (*Amazona vittata*) and the Puerto Rican Plain Pigeon (*Columba inornata wetmorei*). Predation by the RTHA is one of the greatest mortality factors of the Puerto Rican Parrot in El Yunque National Forest (White et al. 2005). My findings can help to identify areas with high concentrations of RTHAs, for example, the southern and southeastern sides of the Luquillo Mountains in order to tailor further reintroduction activities of the Puerto Rican Parrot. The Commonwealth Forest of Maricao on the western side of the Cordillera Central has been proposed as a site to establish a third wild population of the Puerto Rican Parrot (White et al. 2010). However, high abundance of the RTHA and a widespread distribution throughout the region may limit the efforts of reintroduction of this endangered species. Further research aimed at the breeding ecology, movement, and home range of the RTHA in the western

Cordillera Central is needed to improve further conservation and management schemes of the Puerto Rican Parrot in the region.

Table 5.1 Variance Inflation Factor values of the variables Red-tailed Hawk counts in Luquillo Mountains and west side of the Cordillera Central, Puerto Rico during the breeding season of 2012-2013.

Variable	**Luquillo Mountains**	**West Cordillera**
Mean Slope	3.24	2.69
Elevation	1.96	2.25
Canopy Closure	2.62	1.59
Minutes after sunrise	1.02	1.14
Wind Speed	1.14	1.02

Table 5.2 Results from all competing n-mixture candidate set with delta AICc ≤ 2 to describe Red-tailed Hawk counts in Luquillo Mountains, Puerto Rico during the breeding season of 2012-2013.

Model[a]	**Ds**[b]	**df**[c]	**AIC$_c$**[d]	**ΔAIC$_c$**[e]	**cumulW**[f]
1: N_{it} = Cc+Msl+Elv^2, ϕ= Con, r= Cc+Msu	P	8	2239.66	0.00	0.25
2: N_{it} = Msl+Elv^2, ϕ= Con, r = Cc+Msu	P	7	2240.18	0.51	0.45
3: N_{it} = Msl+Elv^2, ϕ= Con, r= Msu	P	6	2241.08	1.42	0.57
4: N_{it} = Cc+Msl+Elv^2, ϕ= Con, r= Cc+Msu	NB	9	2241.67	2.00	0.66

[a] Models are ranked from most to least supported with all including an intercept.

[b] Data distribution either Poisson (P) or Negative Binomial (NB)

[c] Number of parameters with all models containing an intercept term, random term, and an error term.

[d] Akaike information criterion corrected for small sample sizes.

[e] Difference in AICc from the top model.

[f] Cumulative AIC weight.

N_{it} = number of estimated RTHA per survey plot.
ϕ = availableRTHA in a survey plot.
p = detection probability.
Elv^2 = Quadratic effect of elevation.
Cc = Canopy closure.
Msl = Mean slope.
Msu = Minutes after sunrise.
Ws = Wind speed.
Con = Constant.
Ps = Primary survey periods.

Table 5.3 Log-scale coefficients (β), standard errors (SE), significance value (P), and confidence intervals at 95% (LCI, UCL) for covariates of the model number 6 to describe Red-tailed Hawk abundance and detection in Luquillo Mountains, Puerto Rico during the breeding season of 2012-2013.

Parameter	**β**	**SE**	**P(>|z|)**	**LCL**	**UCL**
Intercept (N_{it})	1.418	0.060	<0.001	1.300	1.536
Cc (N_{it})	-0.134	0.085	0.117	-0.301	0.034
Msl (N_{it})	0.227	0.081	0.005	0.068	0.385
Elv^2 (N_{it})	-0.073	0.033	0.025	-0.137	-0.009
Intercept (p)	-1.086	0.059	<0.001	-1.203	-0.970
Cc (p)	0.136	0.065	0.035	0.009	0.263
Msu (p)	-0.172	0.045	<0.001	-0.261	-0.083

Covariates are z-scaled.
Nit= number of estimated RTHA per survey plot.
ϕ = available RTHA in a survey plot.
p = detection probability.
ELV2 = Quadratic effect of elevation.
Cc = Mean canopy closure.
MSL = Mean slope.
Msu = Minutes after sunrise.
WS = Wind speed.

Table 5.4 Results from all competing n-mixture candidate set with delta AICc ≤ 2 to describe Red-tailed Hawk counts in Cordillera Central, Puerto Rico during the breeding season of 2012-2013.

Model[a]	**Ds**[b]	**df**[c]	**AIC$_c$**[d]	**ΔAIC$_c$**[e]	**cumulW**[f]
1: N_{it}= Con, ϕ= PS, r= Ws*Msl	P	8	1687.45	0.00	0.30
2: N_{it}= Con, ϕ= PS, r= Ws*Msl	P	7	1689.37	1.92	0.42

[a] Models are ranked from most to least supported with all including an intercept.
[b] Data distribution either Poisson (P) or Negative Binomial (NB)
[c] Number of parameters with all models containing an intercept term, random term, and an error term.
[d] Akaike information criterion corrected for small sample sizes.
[e] Difference in AICc from the top model.
[f] Cumulative AIC weight.
N_{it} = number of estimated RTHA per survey plot.
ϕ = availableRTHA in a survey plot.
p = detection probability.
Msl = Mean slope.
Ws = Wind speed.
Con = Constant.
Ps = Primary survey periods.
* = Interaction.

Table 5.5 Log-scale coefficients (β), standard errors (SE), significance value (P), and confidence intervals at 95% (LCI, UCL) for covariates of the model number 2to describe Red-tailed Hawk abundance and detection in west side of Cordillera Central, Puerto Rico during the breeding season of 2012-2013

Parameter	**β**	**SE**	**P(>|z|)**	**LCL**	**UCL**
Intercept (N_{it})	1.418	0.060	9.4e-122	-1.203	-0.970
Cc (N_{it})	-0.134	0.085	0.117	-0.301	0.033
Msl (N_{it})	0.227	0.081	0.005	0.068	0.385
Elv^2 (N_{it})	-0.073	0.033	0.02	-0.137	-0.009
Intercept (p)	-1.086	0.060	1.6e-74	-1.203	-0.970
Cc (p)	0.137	0.065	0.034	0.010	0.264
Msu (p)	-0.167	0.046	0.002	-0.257	-0.078

Covariates are z-scaled.
N_{it} = number of estimated RTHA per survey plot.
ϕ = availableRTHA in a survey plot.
p = detection probability.
ELV^2 = Quadratic effect of elevation.
Cc = Mean canopy closure.
MSL = Mean slope.
Msu = Minutes after sunrise.
WS = Wind speed.

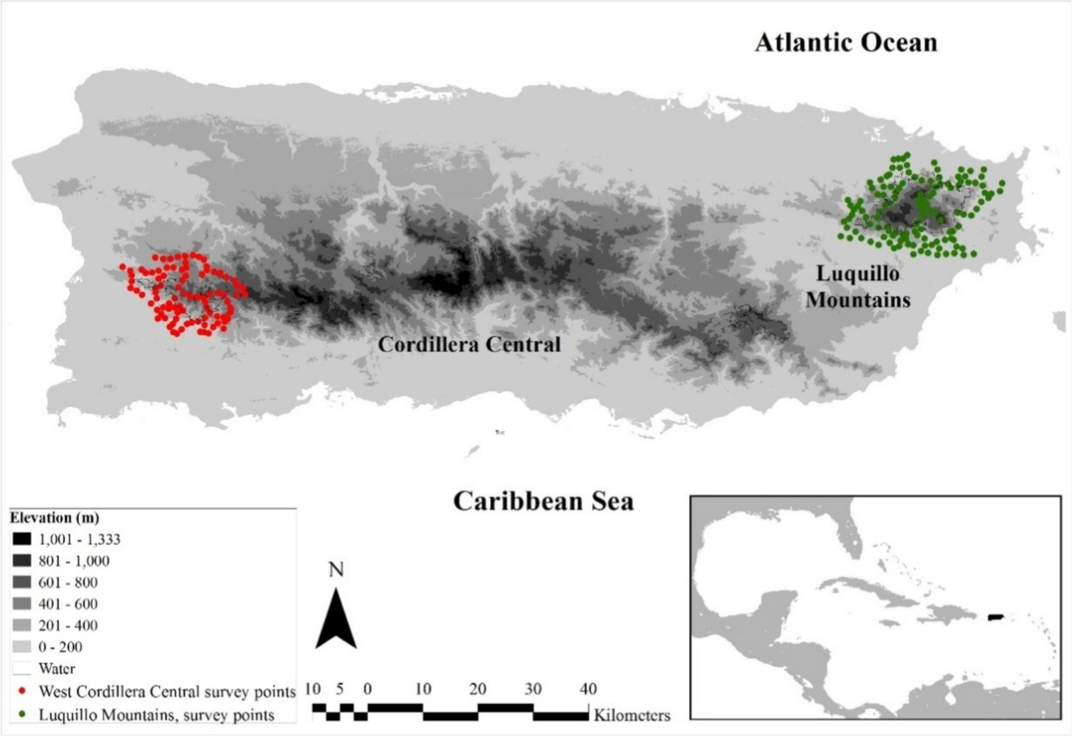

Figure 5.1 Map of Puerto Rico, RTHA survey points, and location in the Caribbean archipelago (inset).

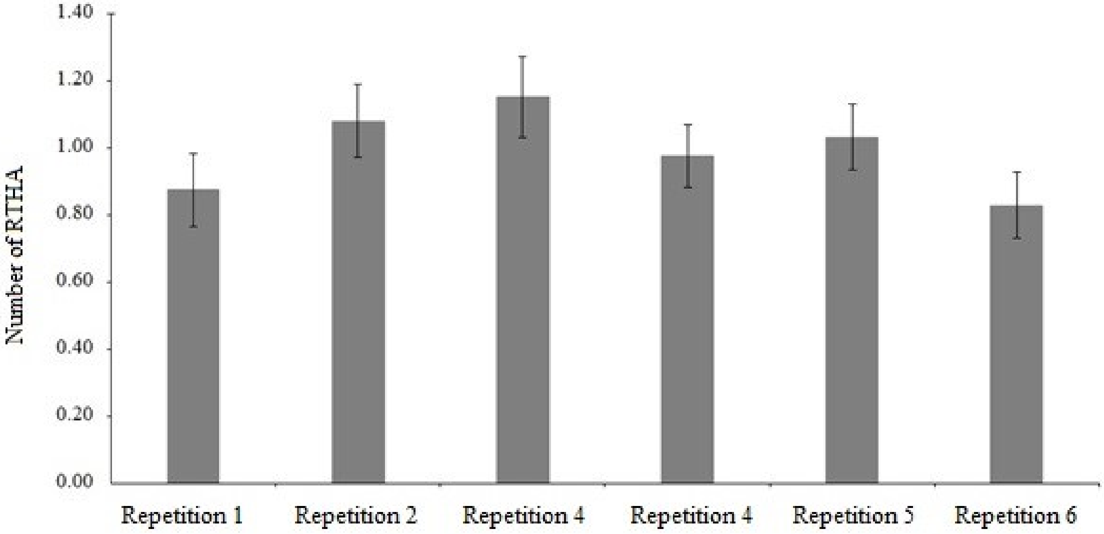

Figure 5.2 Average number of Red-tailed Hawks detections per survey point(Standard error bars) during the breeding season of 2012-2013 in Luquillo Mountains, Puerto Rico.

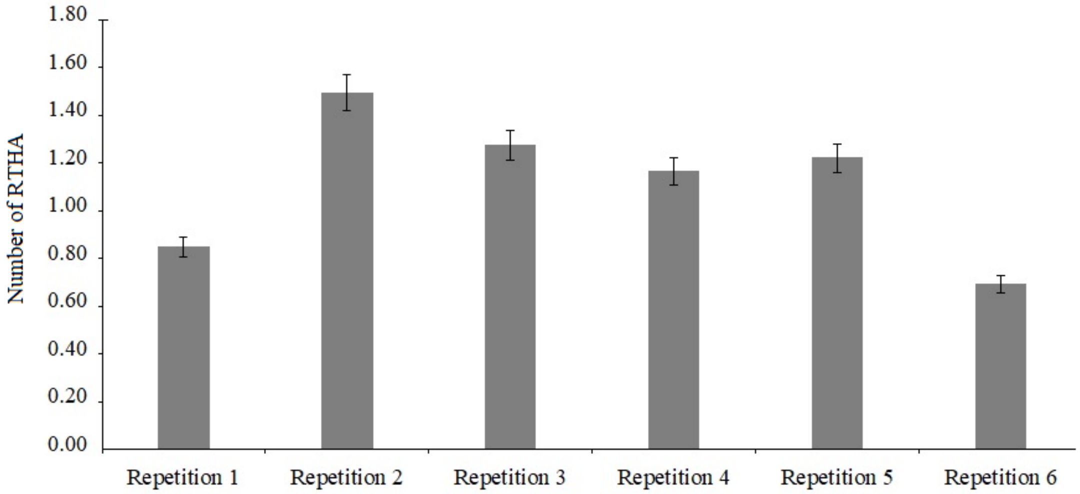

Figure 5.3 Average number of Red-tailed Hawks detections per survey point (Standard error bars) during the breeding season of 2012-2013 in west side of the Cordillera Central, Puerto Rico.

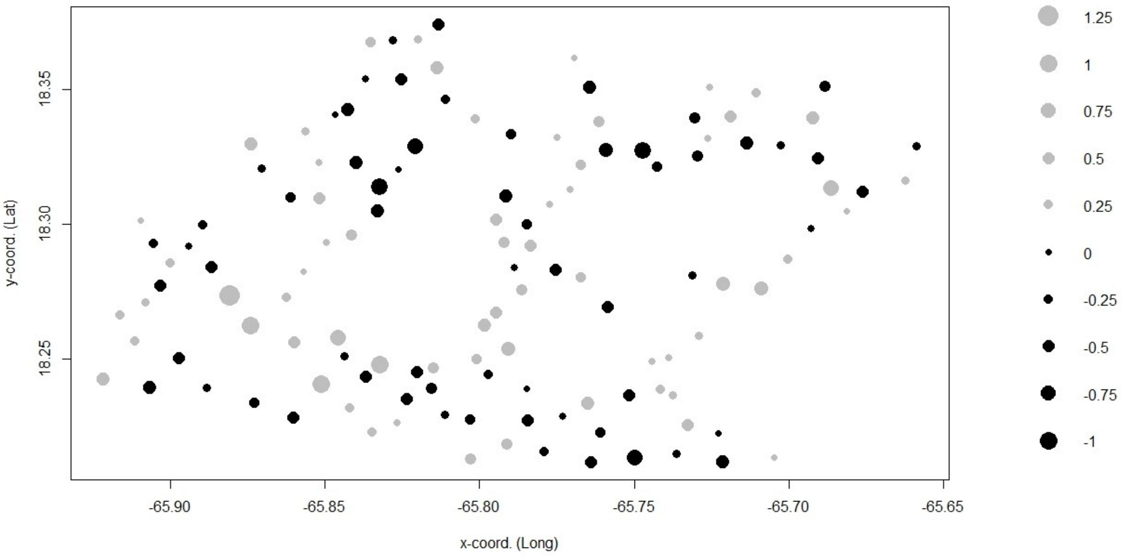

Figure 5.4 Map of residuals (averaged over survey replicates) under ΔAIC-best Poisson model for Red-tailed Hawk counts during the breeding season of 2012-2013 in Luquillo Mountains, Puerto Rico.

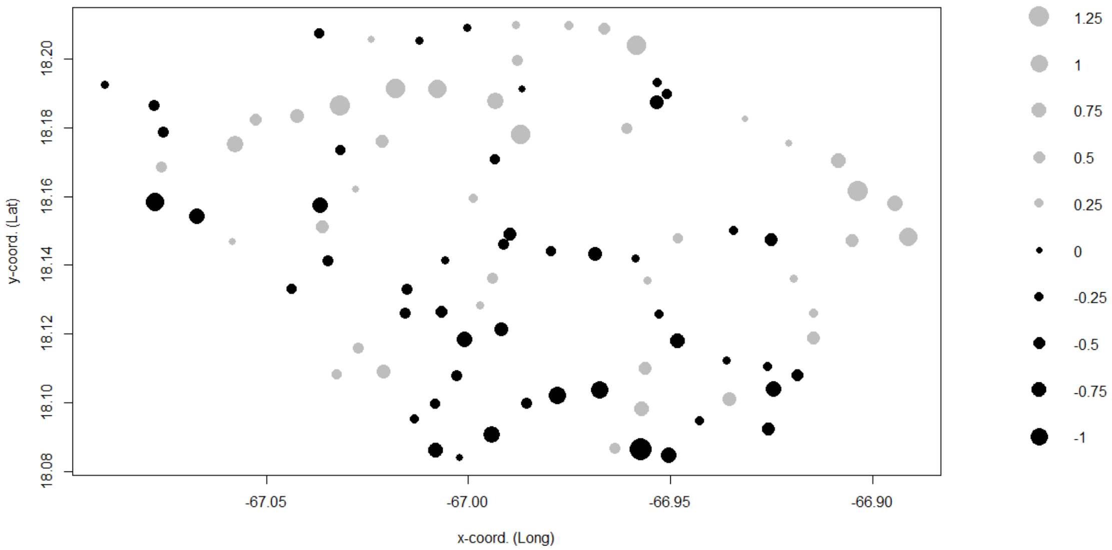

Figure 5.5 Map of residuals (averaged over survey replicates) under ΔAIC-best Poisson model for Red-tailed Hawk counts during the breeding season of 2012-2013 in west side of Cordillera Central, Puerto Rico.

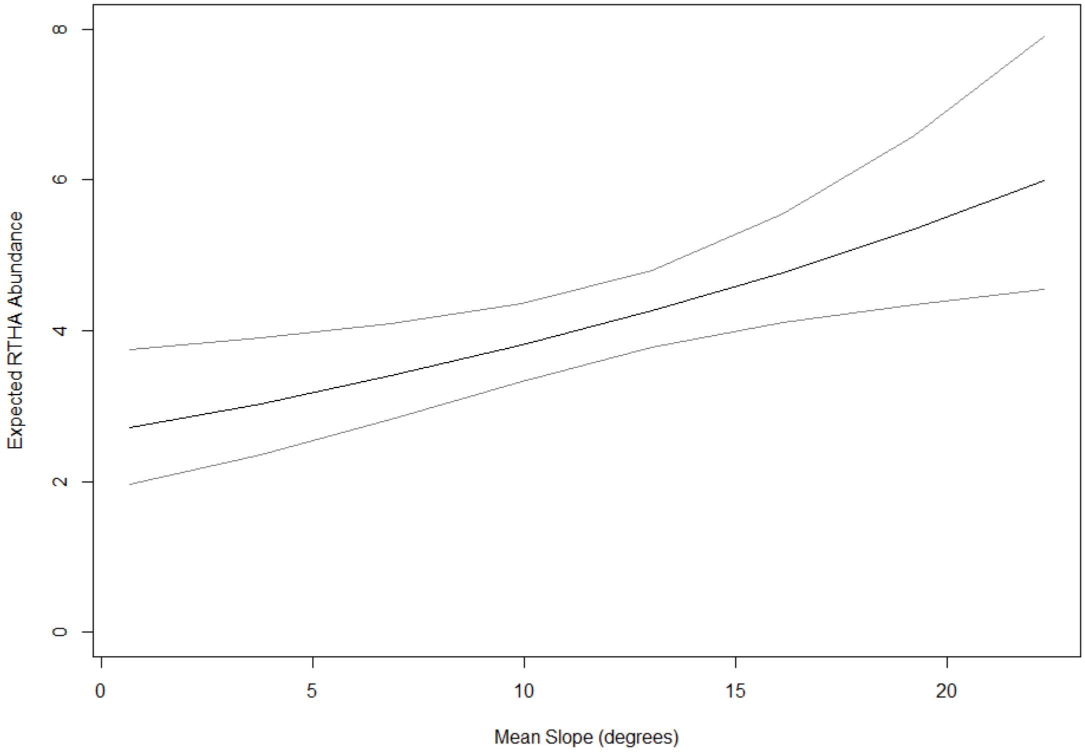

Figure 5.6 Prediction of expected local abundance (survey point) of Red-tailed Hawk by mean slope values during the breeding season of 2012-2013 in Luquillo Mountains, Puerto Rico. Peripherical lines represent 95% Confidence Intervals.

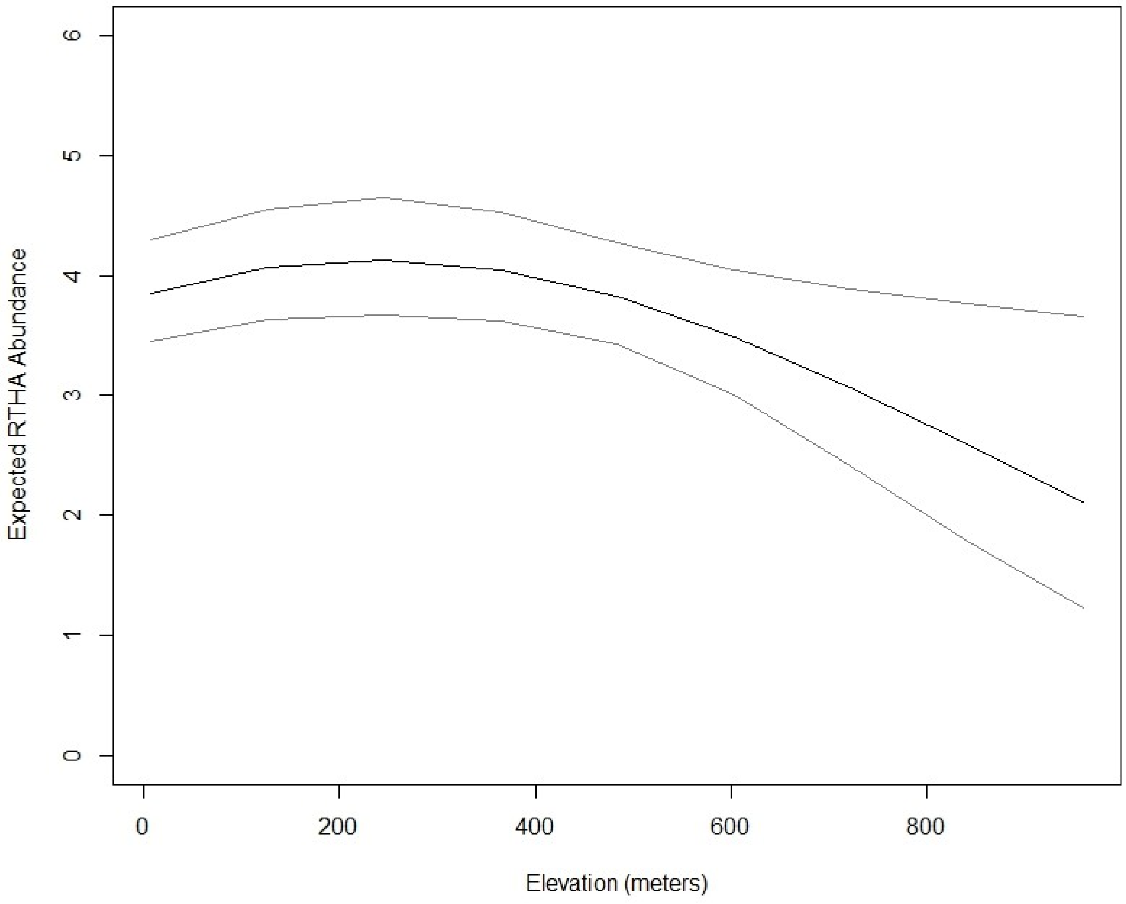

Figure 5.7 Prediction of expected local abundance (N_{ti}) of Red-tailed Hawk by elevation the breeding season of 2012-2013 in Luquillo Mountains, Puerto Rico. Peripherical lines represent 95% Confidence Intervals.

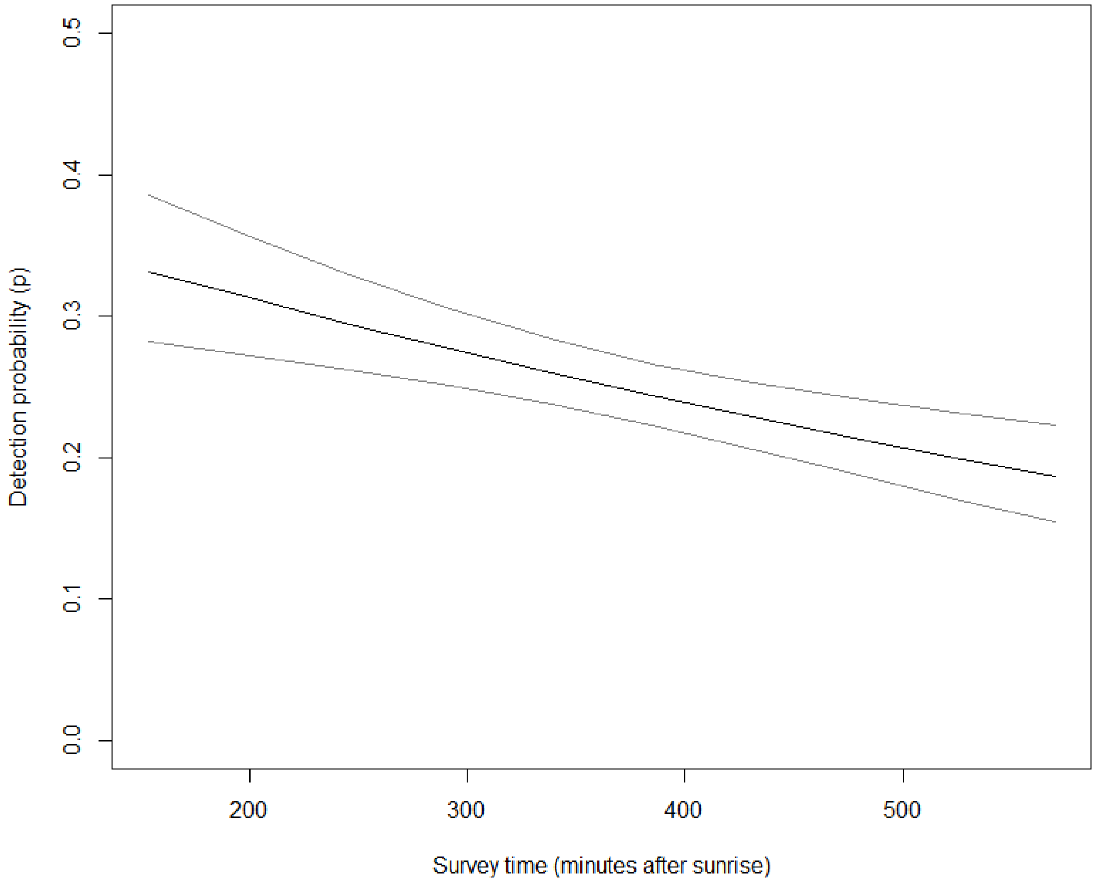

Figure 5.8 Prediction of expected individual detection probability (*r*) of Red-tailed Hawk by survey time (minutes after sunrise) during the breeding season of 2012-2013 in Luquillo Mountains, Puerto Rico. Peripherical lines represent 95% Confidence Intervals.

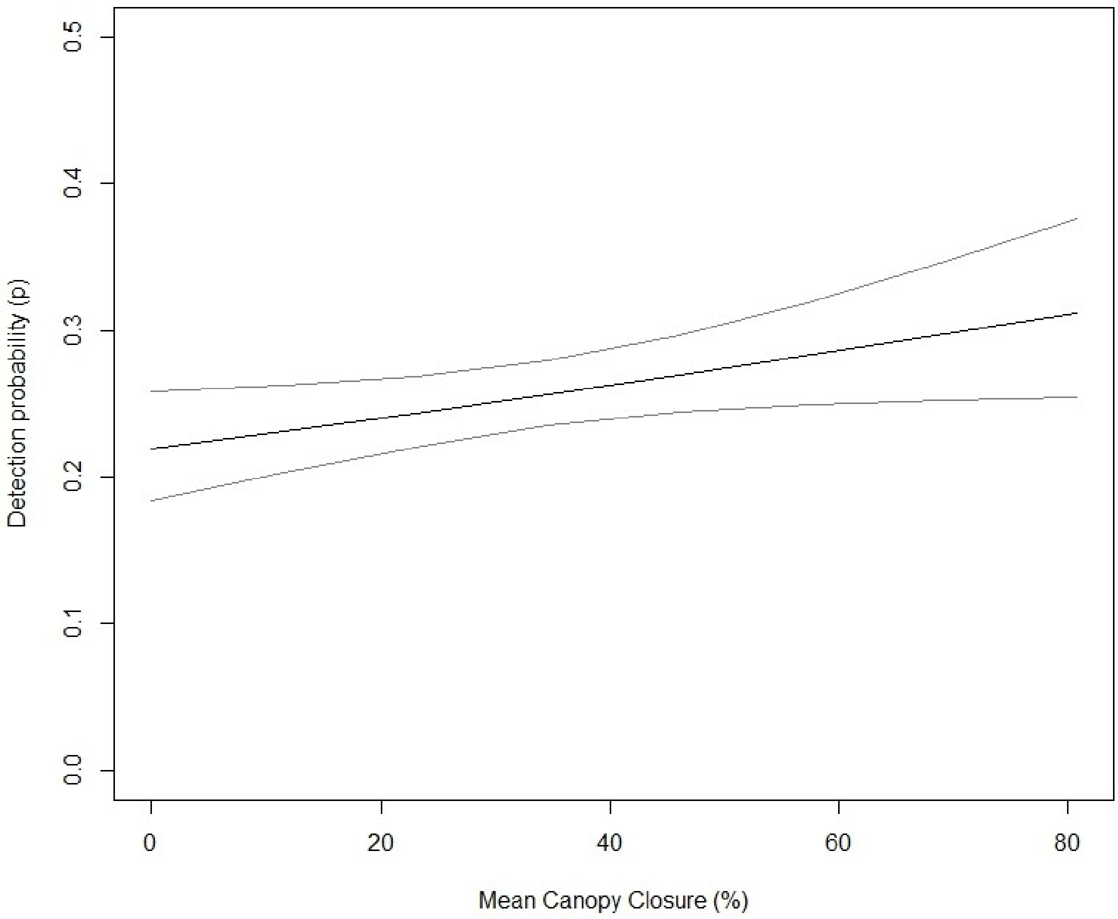

Figure 5.9 Prediction of expected individual detection probability (*r*) of Red-tailed Hawk by Percentage of canopy closure during the breeding season of 2012-2013 in Luquillo Mountains, Puerto Rico. Peripherical lines represent 95% Confidence Intervals.

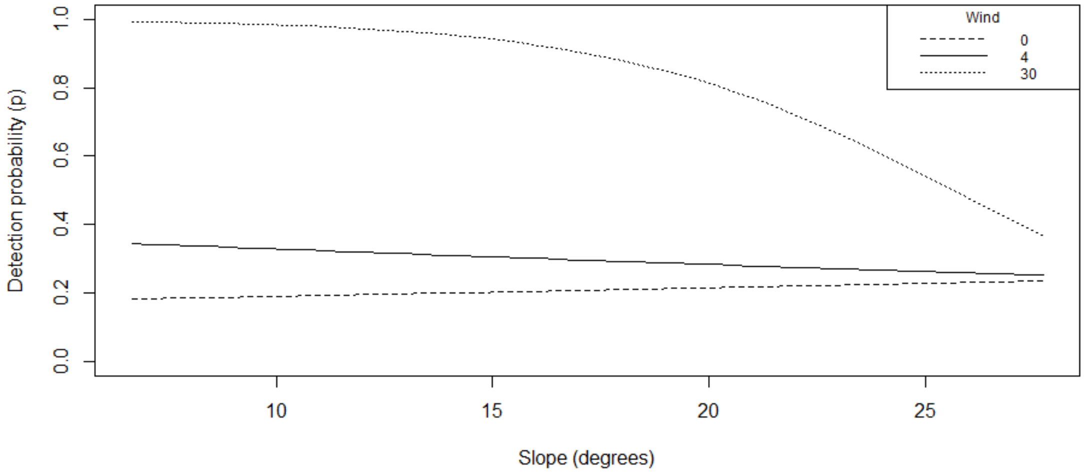

Figure 5.10 Prediction of individual detection probability (*r*) of Red-tailed Hawk by the interaction of wind speed and slope during the breeding season of 2012-2013 in west side of Cordillera Central, Puerto Rico.

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CHAPTER VI

SUMMARY AND SYNTESIS

Summary

Islands are an important repository of global biodiversity as characterized by the preponderance of uniquely specialized forms and great number of endemic species (Myers et al. 2000, Kreft et al. 2008, Donald et al. 2013). However, their limited area (~7% of land surface) puts them at higher risk of perturbation, increasing rate of extinction for some of their taxa (Myers et al. 2000, Keir et al. 2009). Worldwide, approximately 27% of the known species of raptors (~560 spp.; Accipitriformes, Falconiformes, and Strigoformes) are island endemics, except for Australia. This number nearly doubles when island subspecies of continental forms are included (Köing et al. 1999, White and Kiff 2000, Ferguson and Lee 2001). Extinction is not always a random process; some traits manifested in island endemic populations (e.g., restricted ranges, small vital rates, reduced dispersion) may render a greater risk of extinction (Purvis et al. 2000, Krüger and Radford 2008, Donald et al. 2013). Worldwide, six species of raptors have become extinct since the 1600s, four species in the family Strigidae (owls and allies) and two species in the family Falconidae (falcons, caracaras, and allies). All were island endemics and two went extinct as recently as the 20th century (Hume and Walters 2012).

The ecology of the Caribbean Red-tailed Hawk (*Buteo jamaicensis jamaicensis*; hereafter, RTHA) in Puerto Rico is the most documented of all tropical populations of this species (Santana et al. 1986, Santana and Temple 1988, Boal et al. 2003, Nimitz 2005, Llerandi 2006, Vilella and Nimitz 2012). In Puerto Rico, the RTHA appears to retain some vital rates of mainland populations (e.g., clutch size), exhibiting great spatial overlap between territories and the greatest recorded density for the species (Santana and Temple 1988, Boal et al. 2003, Nimitz 2005, Vilella and Nimitz 2012). However, the drivers influencing population dynamics and abundance of this insular subspecies are poorly understood.

The endangered Puerto Rican Sharp-shinned Hawk (*Accipiter striatus venator*; hereafter, SSHA) is a forest-dwelling raptor that was found historically in mature montane forest and timber plantations in the montane regions of Puerto Rico (Snyder and Wiley 1976, Delannoy 1984, Delannoy 1997, Miranda-Castro et al. 2000). The SSHA experienced a 40% population decline in public forests of Puerto Rico, from an estimated 240 individuals in 1985 to 150 in 1991 (Delannoy 1992, Delannoy 1997). Most of the information on ecology, distribution, and population status of the SSHA in Puerto Rico dates from the early 1990s, and no surveys were conducted for this species between passage of Hurricane Georges across Puerto Rico in September 1998, and the work detailed herein.

I examined SSHA potential distribution and landscape variables that may influence it in Chapter III. As part of the Puerto Rico GAP Analysis project Jiménez et al. (2006) used vegetation land cover and elevation as the main criteria to describe SSHA distribution. The resulting model identified 84,859 ha, representing 9.5% of the island's surface, as suitable habitat for this endangered raptor species. The model developed by the PR-GAP project did not consider the species' historical records or sightings, limiting their accuracy and predictions. Conversely, the model I developed affords insight into the geographic distribution of SSHA in Puerto Rico using landscape variables (aspect, canopy closure, elevation, rainfall, slope, and terrain roughness) and known species occurrence locations, representing an improvement over previous models. One of the main findings of this chapter was that the probability of SSHA occurrence (> 60%) was greatest at elevations above 900 m. Moreover, the model predicted more than half of the area most suitable for SSHA is private lands (52.2%; 31.52 km^2), highlighting the importance of land tenure for the conservation of the species. The remaining 43.8% (24.57 km^2) of the predicted area was mostly (~92%) located within three protected areas located in the central and easternmost side of the Cordillera Central. Overall, my model suggests that the potential distribution of the SSHA in Puerto Rico is reduced, isolated, and limited to higher elevations of the main mountain ranges (Cordillera Central, Cayey Mountains, and Luquillo Mountains). Previous studies suggested that the SSHA have small declining populations where most of the breeding territories are located in the Cordillera Central (Delannoy 1997). My results proposed that the current distribution of the SSHA has shrunk and that the area with the greatest probability of occurrence represents approximately 0.6% of the island's surface (56.1 km^2).

Chapter IV modeled population demography of the RTHA in highland forests (above 400 m) and lowland forests (below 400 m) of the Luquillo Mountains. Results indicated both populations exhibited positive discrete rates of growth, with rates of finite population increase (λ) of 1.05 (highlands) and 1.27 (lowlands). Adult survival was the most important parameter influencing population growth (elasticity highland forest = 0.86, elasticity lowland forest = 0.53). The RTHA model showed nestling life stage had the second most important influence on λ (sensitivity lowlands = 0.46, sensitivity highlands = 0.48), emphasizing the importance of early life stages for population growth of the RTHA in the Luquillo Mountains. Differences in nestling survival between highland and lowland forests and their related effect on λ can be partially explained by: a) vulnerability of early life stages to stochastic events (e.g., long periods of fog or rain) that expose nest contents by suppressing parental care, resulting in greater nestling mortality rates at high elevations and consequently, lower value of λ, and b) more open canopy, higher fragmentation, and lower rainfall of lowland forests favoring hunting success and parental care, with resulting higher value of λ. To the best of my knowledge, my approach represented the first use of a periodic matrix (so called seasonal matrix) to describe the annual life cycle of a raptor. This tool may assist conservation and management efforts for species in oceanic tropical islands.

I contributed to further knowledge of raptor ecology in montane forests of a tropical oceanic island by developing RTHA abundance estimation models incorporating environmental (mean slope, elevation, canopy closure) and survey variables (time of day, wind speed, canopy closure) on abundance and detection probability. To reduce bias due to the traits of the RTHA, in Chapter V I developed an open-population n-mixture model for counts of unmarked individuals to generate abundance estimates corrected by detection probability (r) and availability (ϕ). The abundance estimates of the RTHA derived in this chapter were higher than previous estimates for Puerto Rico (Nimitz 2005, Llerandi 2006). Higher abundances of the RTHA were associated with steep slopes at mid-elevations (~300m). These results support my prediction that RTHAs in Puerto Rico may concentrate in areas where individuals can exploit updrafts generated by the prevalent easterly trade winds (Snyder et al. 1987, Boal et al. 2003, Nimitz 2005). This argument may help explain the fact that RTHA abundance on the western side of the Cordillera Central, where the trade winds effect is not as pronounced, was not associated with any landscape variables measured. This suggests lower elevations and smoother slope transitions may encourage a more uniform distribution of RTHAs across the landscape in the western Cordillera Central compared to the Luquillo Mountains. However, further research RTHA spatial ecology is needed to better understand these observed differences in abundance estimates and environmental conditions.

Overall RTHA availability (~1 RTHA/survey site) was constant throughout the length of field surveys for this study and not influenced by the breeding phenology of the species. In the Luquillo Mountains, RTHA detection was negatively correlated to time of day and positively to canopy closure. Canopy closure was related to steeper slopes, where greater RTHA abundance would be consistent with increased detection probability (Newton 1988, Kéry and Royle 2016). Updrafts were an important factor influencing detection probability on the western side of the Cordillera Central, decreasing when strong winds occurred on steeper slopes and lesser wind speeds on gentler slopes.

Conclusion and synthesis

While niche expansion and ecological release exhibited by some island populations can favor a large geographic distribution as seen by the RTHA, lesser dispersion and vital rates may result in habitat and population isolation (traits associated with a high extinction risk) for more specialized birds like the SSHA in Puerto Rico (Pruvis et al. 2000, Krüger and Radford 2008). Understanding the ecological traits and constraints that drive species distribution, population growth, and abundance in island environments is fundamental to enhancing effectiveness of conservation and management approaches. For example, by retaining some mainland population traits (e.g., vital rates) and typical island traits (e.g., adult survival), insular RTHAs in Puerto Rico exhibited sustained population growth, as reflected by their abundance and habitat use. Higher concentrations of the RTHAs in eastern Puerto Rico were associated with steep slopes, a similar pattern documented in other raptor species such as the Black-chested Eagle-buzzard (*Geranoaetus melanoleucus*), and known to prefer steep slopes that allow for more economic flight to hunt and patrol territories (Bustamante et al. 1997).

The formulation for the abundance model used suggests there may always be at least one individual present in a given territory (availability) and that three other individuals are using that same space, for a total abundance of ~4 RTHA/survey site. This may suggest that besides the local resident individuals, other individuals may be using the same area, provided soaring and/or hunting conditions are favorable. A positive rate of RTHA population growth and high annual survival may suggest the presence of a surplus of individuals in the survey areas. Further, high spatial overlap may partially explain the high abundance of the RTHA on the island. Abundance estimates may indicate I surveyed a population composed of non-breeding individuals (floaters) and individuals with extensive territories. Spatial limitation and habitat saturation may prevent some individuals from acquiring a territory (Penteriani et al. 2011). Floaters are commonly present in raptor populations and in some cases play an important role in the population dynamics and persistence of species in a given area (Penteriani et al. 2005, Penteriani and Delgado 2009, Penteriani et al. 2011). High abundance of the RTHA and a potentially high number of floaters may support the replacement of individuals and help maintain stable territories as suggested in previous research (Hunt 1998, Boal et al. 2003). This has special importance in the success of future efforts to recover endangered species areas with high density of the RTHA such as the Luquillo Mountains and the west side of the Cordillera Central. Further research is needed to assess the role of non-breeding individuals in the RTHA population dynamics in Puerto Rico.

My research on the SSHA included a considerable amount of private lands, unlike previous studies. Interestingly, it was in private lands where I found the majority of SSHA individuals. Further, private lands represented the most suitable SSHA habitat. This highlight the critical importance private lands may play in the recovery of the SSHA and the need for collaboration with landowners to develop off-reserve conservation strategies. Further, supporting landscape conservation design projects like the Bosque Modelo of Puerto Rico will greatly benefit SSHA conservation. The Bosque Modelo is an initiative to establish a large-scale biological corridor connecting ecosystems across the western portion of the island. The area proposed for this venture includes the most suitable SSHA habitat identified by my distribution model (Figure 6.1). My model highlights the necessity of conservation actions that include applied research, SSHA population and habitat management, and the engagement of conservation organizations, private landowners, and state and federal agencies to avoid the extinction of the SSHA.

Research aimed at identifying factors that influence population growth and decline of the SSHA and contraction of its geographic distribution should be a priority effort for recovery of the species through its current and historical range. As mentioned earlier, nest predation by the Pearly-eyed Thrasher (*Margarops fuscatus*) and botfly (*Philornis spp*.) infestation were important causes of SSHA nest failure in Maricao Forest and El Yunque Forest. Updated information about their effects on breeding success along an elevation gradient throughout the current and historic SSHA's distribution is needed. Moreover, that information would serve as a baseline to implement any further SSHA population management efforts (e.g., translocations, establishment of new populations) and would be useful for the recovery of others endangered species such as the Puerto Rican Parrot (*Amazona vittata*) (Wunderle and Arendt 2011). The pattern described in my model may be similar for other montane forest-dependent species, especially in the mountains. For example, the endemic and endangered Elfin Woods Warbler (*Setophaga angelae*) has been apparently extirpated from many montane forests and is currently limited mostly to the Maricao Forest and El Yunque National Forest (Anadon-Irizarry 2006, Delannoy-Juliá 2009). Understanding the limiting factors responsible for SSHA population decline and reduction of suitable habitat will help in the development of conservation tools for the recovery of this and other forest-dependent species.

Understanding how population traits and ecological constraints imposed by insular environments affect the distribution, abundance, and population dynamics of species is crucial to implementing management or conservation schemes. Reliable estimates of abundance for a top predator such as the RTHA and the drivers influencing these abundance patterns are particularly important for future restoration plans of the Puerto Rican Parrot in Maricao Forest where the RTHA is as abundant and widespread through the landscape, similar to the Luquillo Mountains (White et al. 2010).Research on spatial ecology and resource use may help design conservation strategies to improve the degree of connectivity of isolated SSHA territories. At the same time, high abundance and a potentially high number of floaters suggest a rapid replacement of RTHA individuals in Puerto Rico, which may limit the success of conservation schemes of endangered species preyed on by this top predator. Further efforts to understand the population dynamics and distributions should be continued to ensure the persistence of the SSHA and to fully understand the impact of the RTHA top predator on other species of the island.

Patterns of island colonization have been studied for several island species, but rarely has the role of evolutionary changes been accounted for in those studies (Newton 2003, Thornton 2007). The demographics and long-distance migratory capabilities of the RTHA may have facilitated the process of colonization of the Greater Antilles and the majority of the Bahamas archipelago. The process of colonization of Puerto Rico by the RTHA could have followed the following steps; a group of individuals displaced from their main migratory route survived in a new wintering area and failed to return to their breeding or resident locations in the mainland the following spring. This phenomenon has been proposed as migration dosing (Bildstein and Zalles 2005). However, neither of these proposed mechanisms have been empirically tested. Migratory individuals from North American populations of RTHA have been reported to reach the Caribbean islands, at least to the Dominican Republic (Keith et al. 2003). However, movement of individuals from mainland populations or between islands has not been evaluated. From ecological and geographical perspectives, the strong selective pressures of island environments and the natural history of the RTHA offer a good opportunity to investigate the role of population dynamics and spatial ecology in the island colonization process of continentally derived raptors. How does population growth influence genetic diversity and do these together trigger dispersion? If some population traits facilitate colonization success and dispersion, do the sesame traits restrict the speciation process? Is Puerto Rico a source population of RTHA for neighboring islands? Answering these questions will require a large sample of genetic material to map the dispersion and colonization events, and how genetic diversity is linked with local abundance and population growth throughout the Caribbean islands.

The distribution of wildlife populations is limited by the amount, arrangement, and distribution of suitable habitat as well by demographic traits that influence local abundance (Newton 1998, Newton 2013). Density-independent (environmental) and density-dependent (demographic) factors can set boundaries of population growth of a given species regarding its biological potential having a direct affect its abundance and distribution (Elton 1924, Nicholson 1933, Nicholson 1954, Andrewartha and Birch 1954). Increasing population rate, high abundance and potentially high number of non-breeding RTHAs may limit vacant territories. Consequently, density-depended factors (e.g., intraspecific competition) may act together to control the species' population growth. On the other hand, the historical population decline and limited geographic distribution of the SSHA may indicate some density-independent factors limit population growth and ecological potential. The combined effect of high rate of nestling mortality from botfly parasitism (*Philornis spp.*) and habitat disturbance following major hurricanes may be important limiting factors may represent ecological inertia restricting SSHA abundance and distribution (Wiley 1986, Delannoy and Cruz 1988, Boose et al.

2004, Flynn et al. 2010). Hurricanes are the most important source of natural perturbation in the Caribbean islands and its effect in population dynamics of the RTHA and SSHA in Puerto Rico has not being assessed (Boose et al. 2004, Flynn et al. 2010). Hurricanes may increase habitat loss, forest fragmentation, and changes in forest structure that limit the amount and distribution of suitable habitat of the SSHA. On the other hand, forest fragmentation and forest gaps may provide suitable habitat that favors RTHA's hunting success.

The effect of controlling limiting factors regulating the population dynamics of SSHA and RTHA in Puerto Rico has not been assessed. Further research is needed to understand the limiting and controlling factors that are governing the population dynamics of RTHA and SSHA in an insular environment. Understand the role non-breeding individuals play in territory dynamics and population growth of the SSHA and the RTHA is needed. Mark-recapture studies would provide reliable information on vital rates, namely survival, allowing inference on territory and population dynamics. Basic information on SSHA movements and resource selection patterns is crucial to understand the magnitude of limiting factors restricting dispersal and connectivity, with consequent negative effects on genetic diversity. Research on SSHA nest predation by Pearly-eyed Thrasher (*Margarops fuscatus*) and parasitism by botflies as potential limiting factors on SSHA populations is critical to design conservation and management schemes. Information to evaluate the effect of current hurricanes (e.g., hurricanes Maria and Irma) is needed, especially to evaluate the potential effect of intraspecific interactions between, for example, displacement or predation of SSHA by RTHA, which is the island's top predator.

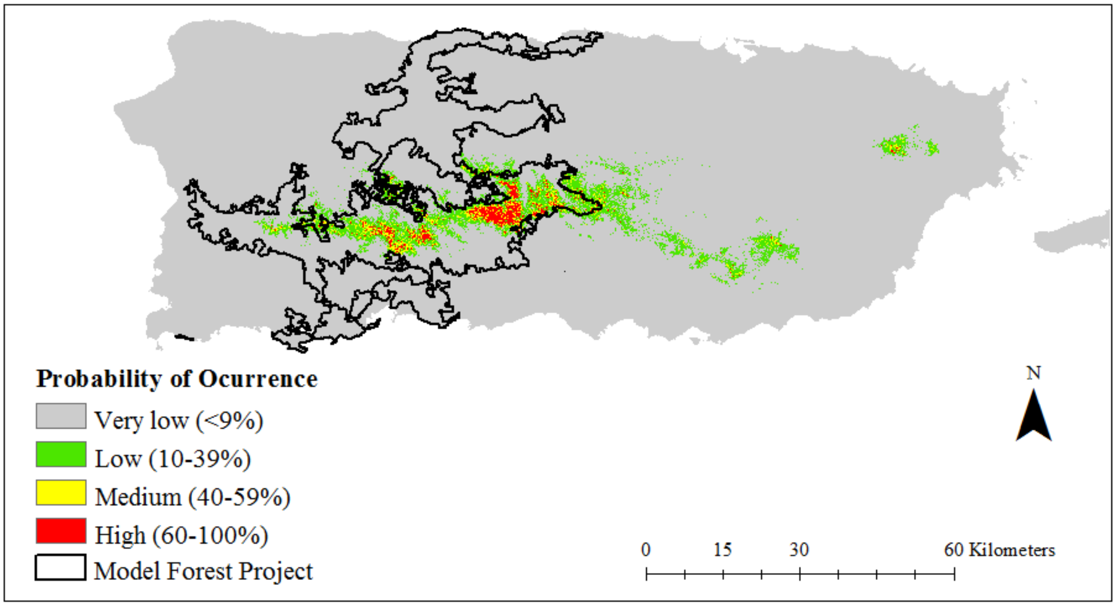

Figure 6.1 Predicted Puerto Rican Sharp-shinned Hawk suitable habitat and the Model Forest Project.

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APPENDIX B

TABLE S1 (Gallardo and Vilella 2017)

Table B.1 Total number of Puerto Rican Sharp-shinned Hawk (*Accipiter striatus venator*) observed by municipality, land tenure, elevation, and year the territory was located from 2013 to 2016.

Territory Name	Number of Individuals	Elevation (m)	Land Tenure or Protected Area	Breeding Season
Chihuahua	1	816	Private	2016
Jayuya	1	1212	Private	2014, 16
143.1	3	1059	Private	2016
143.2	2	1200	Private	2016
JG-SSHA-5527	1	811	Private	2016
SSHA ADJ 03	1	953	Private	2014, 16
Bruma-1	2	1132	Private	2016
VACA01	2	868	Private	2016
Roncador04	2	673	Private	2016
Chihuahua2	1	729	Private	2016
Foreman	2	642	Private	2014, 16
Cerrote1	1	868	Private	2016
ESC01	2	619	Private	2016
Choco	2	778	Private	2014, 16
Garze03JCG	1	797	Private	2016
144-02	1	656	Private	2016
Camino Noriega	1	535	Private	2013
Indios	1	392	Private	2013

Table B 1. (continued)

Territory Name	Number of Individuals	Elevation (m)	Land Tenure or Protected Area	Breeding Season
Carrite5-1	1	770	Guilarte Forest	2016
Missing Choco	2	938	Guilarte Forest	2016
AdjuntasGar-01	1	896	Guilarte Forest	2016
C7	2	860	Maricao Forest	2013, 14, 16
Campground 1	2	858	Maricao Forest	2013, 2014, 16
Campground 2	2	873	Maricao Forest	2016
Maricao Office	2	741	Maricao Forest	2013, 14, 16
Guineo	2	903	Toro Negro Forest	2016
Rose House	3	1019	Toro Negro Forest	2016
Cerro Rosa	2	1134	Toro Negro Forest	2016
Toro 1	3	903	Toro Negro Forest	2014, 16
Cristo Viene	2	1098	Toro Negro Forest	2014, 16