ECOLOGY AND CONSERVATION GENETICS OF RIDGWAY'S HAWK *Buteo ridgwayi*

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ABSTRACT

Ridgway's Hawk is a forest raptor endemic to the island of Hispaniola in the West Indies. The species is ecologically little known, with only three nests followed in 1976, and no comprehensive nest observations reported since then. This thesis reports on 5 years of research on the ecology and conservation genetics of this small isolated population.

The global distribution was found to be limited to an area of 1600 km^2 on the northeast coast of the island, with only one source population. Population size was estimated at 91-109 breeding pairs remaining with a continued declining trend observed over the study period. Effective population size for the species may be less than 40 individuals.

Breeding pairs were found to be socially and genetically monogamous. Nests were constructed in native palm or hardwood trees, in areas with both intact secondary forest and small agricultural plots. Productivity averaged 0.64 young fledged per nest, similar to that of other tropical raptors. Nestling sex-ratio showed a trend toward female bias.

Ridgway's Hawk relied on reptile prey for ~80% of the diet as well as rats (9%) and smaller proportions of birds, frogs and arthropods. This specialist reptile diet provides insight into the current distribution of the species in the wet lowland forest of Los Haitises, where reptiles are abundant.

Human activities including poaching of nestlings and habitat conversion within Los Haitises National Park are the main threats to the current population with sixty percent of nests monitored failing due to human activities.

Genetic diversity within the population, based on 11 microsatellite loci, was found to be relatively high with a mean heterozygosity of 0.732. Deviations from Hardy-Weinberg equilibrium and linkage disequilibrium were found for several loci, with inbreeding as the most likely source of these deviations. Supporting evidence of inbreeding was verified by genetic relatedness estimators that showed 4 of 8 sampled pairings and up to 18% of potential pairings to be inbred.

Conservation of the species is highly dependent on the protection of the remaining forested area of Los Haitises National Park. Although more intensive management will be required within the immediate future, high productivity and an ability to use human altered habitat has allowed this hawk to persist. If provided with a safe forested area, free from human persecution, and ample reptile prey, the population could recover.

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I would like to dedicate this thesis to the memory of Frances Nichols.

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Chapter 1

INTRODUCTION AND CONTEXT: ECOLOGY AND CONSERVATION GENETICS OF RIDGWAY'S HAWK *BUTEO RIDGWAYI*

1.1 GENERAL INTRODUCTION

The island of Hispaniola is located in the Greater Antilles of the West Indies. It is comprised of the sovereign states of Haiti and the Dominican Republic. Hispaniola is of international priority for conservation science due to its unique biological diversity and a high degree of threat to the endemic flora and fauna (Myers et al. 2000). The unique avifauna was first described in detail during the late 19th and early 20th century by Charles Cory, James Bond, Alexander Wetmore and Bradshaw Swales (Cory 1885, Bond 1928, Wetmore & Swales 1931). This avifauna is particularly distinct with six endemic genera, and is one of the highest rated Endemic Bird Areas in the world (Stattersfield et al. 1998). The research presented in this thesis aims to address the lack of knowledge on the ecology, genetics and population status of Hispaniola's only endemic raptor, Ridgway's Hawk *Buteo ridgwayi*, and to make conservation recommendations for its future survival.

Buteo ridgwayi is ecologically little known. The population has vastly diminished in range and numbers from its status just a century ago (Wiley & Wiley 1981). If the factors threatening this rare species are to be identified and mitigated, it is essential to understand the basic ecology and population genetics of *B. ridgwayi*.

Similar patterns of population decline and loss have been observed globally for endemic island birds (Myers 1979). The current research presents an opportunity to look at the effects of a rapid population decline on the population genetics of an island endemic. The results and recommendations from this study of *B. ridgwayi* will be applicable to other endangered avifauna, particularly raptors. This thesis uses a multifaceted approach, combining conventional ecological techniques with focused molecular approaches to population genetics. This combined approach has advantages over single discipline studies and is applicable in wider conservation contexts. This thesis constitutes the first detailed study on the ecology and population genetics of this species, and ultimately, was carried out to make conservation recommendations to ensure its continued survival. It is quite probable that the future survival of Ridgway's Hawk will require escalating levels of intensive management within an increasingly human altered environment. This will require protection of dwindling forest fragments, captive breeding, and translocation of the species to human altered habitats. This thesis documents the species' biology and ecology within the remaining karst rainforest of Hispaniola prior to intensification of management efforts.

1.2 THE WEST INDIES

1.2.1 Geological history and biogeography of the West Indies

The West Indies is an archipelago of approximately 7,000 islands in the Caribbean Sea and consists of the Bahamas, the Cayman Islands, the Greater Antilles (Cuba, Jamaica, Hispaniola, Puerto Rico), and the Lesser Antilles from the northernmost island of Anguilla to the southernmost island of Grenada. The Greater Antilles are older than the emergent Lesser Antilles with islands in the Greater Antilles being made up of continental rock, and the Lesser Antilles being primarily coralline or volcanic in origin (Rosen 1976).

The biota of the West Indies exhibits a very high level of diversity and endemism (Myers et al. 2000), particularly among vertebrate species (73% endemicity). This is due in part to a complex geological history. A combination of tectonic events, changes in sea level, a meteor impact, and proximity to North, Central and South America have affected species divergence, dispersal and extinction (Rosen 1976, Bond 1978, Morgan & Woods 1986, Davalos 2004). A feather found in 15-20 million year old amber from Hispaniola indicates that birds were already present in the Greater Antilles by the late Miocene (Laybourne et al. 1994). Ancestors arrived by over-water dispersal events from the mainland, with dispersal occurring from North and Central America (Lack 1973, Bond 1978, Olson 1978, Hunt et al. 2001).

1.3 THE ISLAND OF HISPANIOLA

1.3.1 Physical and climatic characteristics of Hispaniola

Hispaniola (19° 0' N 71° 0' W) is located in the center of the Greater Antilles archipelago (Fig 1.1) and consists of the nations of Haiti and the Dominican Republic. The Dominican Republic occupies the eastern two-thirds of the island and the two nations share a 360km border. Hispaniola is *c.*78,400 km^2 in size, the second largest island in the West Indies after Cuba.

Hispaniola hosts the highest and lowest elevations in the West Indies, from 40 m below sea level at Lago Enriquillo to >3,000 m above sea level at the summit of Pico Duarte. This varied topography has created a diverse range of habitat types from desert scrub to coastal rainforest to high elevation pine forest, which has also contributed to the high faunal species diversity and endemism.

Hispaniola has a seasonal tropical climate with significant regional variation in temperature and rainfall due to the size and topography of the island. Temperatures along the coast range from 20°C at night to 31°C during the day. The interior mountain ranges are considerably cooler, with lows <0°C and highs of *c.*16°C. Desert regions in the southwest Dominican Republic experience the highest temperatures reaching >40°C, and lowest amounts of annual rainfall, <500 mm. The cool, wet season is from April-December with eastern regions of the island receiving >2000 mm of annual rainfall. Humid wet forests receive the highest annual amounts of precipitation of >3000 mm. Hispaniola is within the hurricane belt of the West Indies. The peak hurricane season is August-September.

1.3.2 Human impact on Hispaniola

The impact of humans on the islands of the West Indies has been severe. The islands of the Greater Antilles once hosted a unique evolutionary branch of primates and at least four genera of sloths (MacPhee et al. 2000, MacPhee & Meldrum 2006). The islands also supported an astonishing diversity of native insectivores and rodents including giant hutias and spiny rats (MacPhee et al. 1999, White & MacPhee 2001)

Hispaniola alone was once home to more than 25 species of endemic terrestrial mammal (MacPhee & Iturralde-Vinent 2000). Only two remain, the Hispaniolan Hutia *Plagiodontia aedium* and the Hispaniolan Solenodon *Solenodon paradoxus*, and both are threatened with extinction. Several avian species have gone extinct including an endemic giant barn owl *Tyto ostologa* and a cave rail *Nesotrochis steganinos*. Subfossils have been found of giant raptor species including a Titan hawk *Titanohierax* sp. and a giant eagle *Amplibuteo* spp. (Olson & Hilgartner 1982, Suárez 2004).

Between 1630 and 1880, vast areas of lowland forest were converted to sugarcane. Following the abolition of slavery in the 1880s, the human population spread to the mountains and degradation of the montane forest began (Harcourt & Sayers 1996). Less than 1.5 % of Haiti's original forest is left, most of which is in the inaccessible uplands of the island and is highly degraded (Rimmer et al. 2005). The Dominican Republic has not fared much better with only 10% of its original forest cover remaining under threat to further loss from unregulated logging, slash-and-burn agriculture, and charcoal production (Latta et al. 2006).

Hispaniola's ecosystems have been further modified by the introduction of exotic fauna and flora. Free-ranging cattle, goats and wild pigs have changed the landscape while feral cats, dogs and the introduction of Ship Rats *Rattus rattus* in the 15th century and the Small Indian Mongoose *Herpestes auropunctatus* in 1872 have undoubtedly played a major role in the extinctions of native species. These introduced predators continue to have an impact on native avifauna to this day (Rimmer et al. 2008).

1.3.3 Biodiversity of extant Hispaniolan vertebrates

Hispaniola's unique biodiversity has earned it one of the highest levels in a world-wide assessment of conservation priorities (Stattersfield et al. 1998). There are currently 20 mammal species: the Hutia, Solenodon, and 18 species of bat. The endemic herpetofauna of Hispaniola is extremely diverse with 64 amphibian and 153 reptile species (Powell et al. 2000), with new species still to be described and even discovered (E. Fernandez pers. comm.). Ninety-two percent of Haitian amphibians are threatened with extinction (IUCN 2010).

The island has a particularly distinct avifauna with six endemic genera (Stattersfield et al. 1998). To date, 306 bird species have been recorded for Hispaniola including 140 breeding residents and 136 species of Neotropical migrants that over-winter on the island (Perdomo & Arias 2009). Thirty-two species and 52 subspecies are endemic (Latta et al. 2006), 16 of which have threatened status and six of which are considered near threatened (IUCN 2010).

1.4 DISTRIBUTION AND STATUS OF THE GENUS Buteo

The Genus *Buteo* is widely distributed and occurs on all continents except Antarctica and Australia. The Genus comprises 28 species (Thiollay 1994), 21 of which are found in the New World (Ferguson-Lees & Christie 2001).

Three species of *Buteo* are island endemics: the Galapagos Hawk *B. galapagoensis*, the Hawaiian Hawk *B. solitarius* and Ridgway's Hawk. Amaral et al. (2009) supports speciation of these island *Buteos* through loss of migration, since their ancestors were hypothesized to be migratory. Bildstein (2004) termed this process 'migration dosing' where migrants were displaced, possibly by adverse weather conditions. These vagrants were then unable to return to their mainland breeding grounds, became established and subsequently speciated. Fossil remains of the Red-shouldered Hawk *B. lineatus*, which is currently distributed in the eastern and southern United States, southern Canada and northern Mexico, have been found in Cuba (Suarez & Olson 2003) and recent molecular evidence (Amaral et al. 2009) suggests that *B. lineatus* is the continental ancestor of *B. ridgwayi.* If this was the case, the original colonization event was followed by a dramatic decrease in body mass. Adult *B. lineatus* are *c.*170-180% heavier than *B. ridgwayi* (Dykstra et al. 2008, this study). This speciation trend has also been observed for the

Hawaiian Hawk, where the ancestral species, hypothesised to be Swainson's Hawk *B. swainsoni* (Riesing et al. 2003), is 177-200% larger than *B. solitarius*.

Four of the 28 *Buteo* species are classified with threatened or near-threatened status (IUCN 2010). Three of these are the island endemic species. The Galapagos Hawk is 'Vulnerable' and both the Hawaiian Hawk and the Rufous-tailed Hawk *B. ventralis*, which is found in southern Chile and Argentina, are 'Near Threatened' due to restricted ranges and small population sizes. The population trends for all three species appear to be stable at the moment, but an uplisting would be warranted if any signs of decline were observed. Ridgway's Hawk is the rarest *Buteo*, listed as Critically Endangered (IUCN 2010) due to a small, rapidly declining population.

There are two resident *Buteo* species on Hispaniola. The much larger Red-tailed Hawk *Buteo jamaicensis* is native to the West Indies (as well as North and Central America) and resident on most of the islands in the archipelago (Bond 1979), and is represented in Hispaniola by the subspecies *B. jamaicensis jamaicensis* (Latta et al. 2006). Little is known about the interactions between these two species. However, the Red-tailed Hawk is more widely spread over a variety of open habitat types and not a forest specialist like Ridgway's Hawk. Prey taken by Red-tailed Hawks in Hispaniola were primarily rats and medium-sized birds (Wiley & Wiley 1981), while Ridgway's Hawk rely heavily on skinks, anoles, and snakes (Wiley & Wiley 1981, this study). This lack of overlap in resource use may explain the co-existence of the two *Buteo* species on Hispaniola. It is worth noting that the Broad-winged Hawk *Buteo platypterus* is a forest specialist that is resident on several Caribbean Islands including Cuba, Puerto Rico, and the Lesser Antilles but has only been recorded as a vagrant on Hispaniola (Latta et al. 2006).

1.5 THE STUDY SPECIES: Ridgway's Hawk *Buteo ridgwayi*

Ridgway's Hawk (Cory 1883) is a medium-sized forest raptor endemic to Hispaniola and its surrounding satellite islands (Wetmore & Lincoln 1934, Wiley & Wiley 1981). The adult plumage consists of brown-grey upperparts, greyish barred underparts with reddish-brown wash, rufous thighs, and a brown-and-white barred tail. The adult male is slightly smaller than the female (see Chapter 8), with a greyer head and belly, and a stronger rufous colour on the shoulders and thighs (Fig 1.2).

Ridgway's Hawk has been recorded from a number of habitats including rainforest, dry scrub forest and mixed agricultural-secondary forest (Wiley & Wiley 1981). Previous knowledge of the species' ecology was based on detailed observations of three pairs carried out in 1976 by Wiley & Wiley (1981). Territorial display flights began in January with nest construction in February. Average territory size for the three pairs was 57.8ha. Clutch size was 1-2 eggs and incubation carried out primarily by the female. Nestlings fledged during the 12th week after egglaying. Both sexes defended nests against intra- and inter-specific intruders. Prey items were primarily lizards, snakes, and small mammals, but smaller birds and bats were also fed to nestlings.

Ridgway's Hawk were locally common throughout Hispaniola at the turn of the century, particularly on the larger satellite islands of Haiti and along the northeastern coast of the Dominican Republic (Cory 1885, Wetmore & Lincoln 1934) but all observers documented a rapid decline throughout the range during the first half of the 20th century (see Chapter 3). The last Haitian record for the species was a series of museum specimens collected on Île à Vache on August 4, 1962 by A. Schwartz. During the 1990s the species was considered to be near extinction with nearly all known historical localities extirpated or available forest habitat destroyed. Only a few pairs were known from Los Haitises

National Park (Nigel Collar in litt. 2004). Surveys in 2002-2003 by Thorstrom et al. (2005) documented that a small population remained within Los Haitises National Park on the northeastern coast of the Dominican Republic. In 2006, the total population estimate for Ridgway's Hawk was 80-120 pairs (IUCN 2010). The current distribution of *Buteo ridgwayi* is limited to the heavily fragmented and rapidly disappearing karst rainforest of Los Haitises National Park in the northeastern Dominican Republic (see Chapter 3).

Annual surveys have been carried out since 2002 by The Peregrine Fund (TPF) and Sociedad Ornitólogica Hispaniola (SOH) to assess the distribution of nesting pairs of Ridgway's Hawk in Los Haitises (Thorstrom et al. 2005, 2007). A community awareness program was also carried out by these organisations in 2007, which involved the distribution of posters and a series of community theatres in villages near the remaining hawk population. More recently in 2008-2009, TPF and SOH have been trialing translocation of a small number of juveniles to private lands at Loma La Herradura *c.*30km east of Los Haitises, and Punta Cana *c.*130km southeast of Los Haitises.

Ridgway's Hawk tissue samples have been included in molecular studies of raptor phylogeny (Riesing et al. 2003, Amaral et al. 2009), the results of which suggest that Ridgway's Hawk's closest relative is the Red-shouldered Hawk.

1.6 POPULATION GENETICS OF ISLAND ENDEMICS

Island populations, like that of Ridgway's Hawk, have a higher risk of extinction than mainland populations (Smith et al. 1993). Ninety percent of bird extinctions in historic times have been on islands (Myers 1979). Susceptibility of island birds to extinction is primarily related to habitat loss, persecution and introduction of exotic species (Olson

1989) and genetic factors affecting small populations (Frankham 1995a, Frankham 2005).

Genetic variation provides populations the ability to evolve in response to environmental change. Genetic variation in a population is continually being created by mutation and at the same time being decreased by natural selection and genetic drift (Frankham et al. 2002). Although the impact of random allele loss through genetic drift is minimal within large natural populations, small isolated populations with lower levels of genetic variation (Eldridge et al. 1999) can be threatened by allele loss (Lowe et al. 2004). To ensure long-term viability, a population must be sufficiently large to be able to cope with demographic and environmental stochasticity, and processes that can lead to genetic deterioration such as inbreeding and mutational meltdown (Lande 1995, Lynch et al. 1995).

Ridgway's Hawk has undergone a dramatic range contraction during the last century (Wiley and Wiley 1981). The restricted range and small population size of <120 pairs (IUCN 2010) make Ridgway's Hawk vulnerable to the general underlying patterns of small population genetics. Population bottlenecks and fragmentation lead to even smaller, isolated populations. Fluctuations in effective population sizes, genetic drift, and reduced gene flow could all result in reduced genetic variation and inbreeding depression (Crnokrak & Roff 1999, Hedrick & Kalinowski 2000, Keller & Waller 2002). This could lead to high extinction risk from lowered fitness and an inability to adapt to rapid changes in environmental conditions (Frankham 1995b, Frankham 1998, Reed et al. 2003, Blomqvist et al. 2010, Bolund et al. 2010).

Conservation genetics is an applied science, involving the application of molecular genetics to the conservation of biodiversity (Frankham 2010). Currently one of the top priorities in this discipline is ‘to institute rational genetic management of threatened species in the wild’, particularly for small, isolated or fragmented populations (Frankham 2010). If genetic factors are not taken into account, extinction risks may be underestimated and inappropriate recovery strategies implemented (Frankham 2005, 2010). The maintenance of genetic variation is a critical aspect of any conservation management strategy. This thesis examines the genetic diversity and structure of this small, declining population to assess the potential risks of extinction to Ridgway’s Hawk from genetic factors.

1.7 PROPOSED RESEARCH

1.7.1 Research objectives

The specific research objectives of this thesis were to:

- Estimate the global distribution, population size and trends for Ridgway’s Hawk
- Investigate breeding ecology to identify whether the inherent biology of Ridgway’s Hawk (breeding episode, productivity, survival) was contributing to the species decline
- Examine food resource use and provisioning rates
- Characterise genetic diversity within the remaining population
- Verify the social mating system and determine the genetic mating system of breeding Ridgway’s Hawk
- Ascertain genetic relatedness among individuals, particularly breeding pairs
- Identify threats and factors (environmental, social, demographic and genetic) affecting survival of the remaining population

- Make recommendations for conservation management

1.7.2 Scientific significance of the current study

Seventy-six percent (222) of the world's species of diurnal raptors are found in the tropics (Bildstein et al 1998) Although raptors are much more diverse in the Neotropics (67 genera) than in North America (14 genera, Bildstein et al 1998), a relatively small number of ecological studies have been carried out on Neotropical raptors, particularly in the West Indies (Wiley 1986) The proposed research will add to the currently limited knowledge of tropical raptor ecology

The majority of studies that have examined avian genetic variation have looked at widespread mainland species (Mock et al 2002, Van Den Bussche et al 2003, Godoy et al 2004, Martinez-Cruz et al 2004, Johnson et al 2004) There has been a gradual increase in research on island endemics (Triggs et al 1989, Ardern & Lambert 1997, Tarr et al 1998, Tarr & Fleischer 1999, Groombridge et al 2000, Nichols et al 2001, Boessenkool et al 2007, Groombridge et al 2009) In general, endemic island species show higher rates of historical extinction (Johnson & Stattersfield 1990) and lower genetic variation (Frankham 1997) than mainland populations This thesis provides an opportunity to examine the effect of an extensive and rapid decline in population distribution and size on the genetic diversity of an endemic island species

This thesis takes a multi-faceted approach, combining standard ecological methodologies with molecular techniques to describe the factors which have lead to the decline of a species This multi-disciplinary approach can be transferred and applied to the research of other threatened species facing rapid population declines

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Figure 1.1 Map showing location of Hispaniola in the West Indies. Modified from image at http://alabamamaps.ua.edu.

Figure 1.2 Photograph of an adult female and adult male Ridgways' Hawk. Female in foreground. Photo by Lance Woolaver.

Chapter 2

STUDY SITE AND GENERAL RESEARCH METHODOLOGIES

This chapter describes the research timeline, study area, and general methodologies for field and laboratory research. Specific methodologies are detailed within each relevant chapter.

2.1 RESEARCH TIMELINE

A preliminary reconnaissance to Hispaniola was carried out from February-April of 2004 to assess the feasibility of the proposed research. Field research was then carried out during five continuous field seasons from January-July from 2005 through 2009, covering the breeding season for Ridgway's Hawk. Field work was conducted by the author and three local research assistants; Timoteo Bueno Hernandez, Hilario Jorge Pollanco and Pastor de Leon Franco. Data were also collected by field research assistants in 2005 (Jennie Sinclair and Todd Nichols) and 2006 (John Vetter).

Molecular work was carried out in September-December of 2006 through 2008. All molecular work was carried out in the Molecular Lab at York University (YUMEL) by the author.

2.2 DESCRIPTION OF STUDY AREA

2.2.1 Los Haitises

Los Haitises National Park (19° N 70° W) ranges from 0-380m asl in elevation and is located on the northeast coast of the Dominican Republic (Figure 2.1). The Los Haitises mountain range was formed during the Miocene (Zanoni et al. 1990). It is a platform karst (eroded limestone) formation, with dense clusters of steep conical hills, or mogotes, of nearly uniform height (200–300 metres) separated by sinkhole valleys (Figure 2.2). The Los Haitises region consists of thousands of such mogotes within an area of *c.*1600 km^2.

The mean temperature of Los Haitises ranges from 25-30°C. Los Haitises is affected by trade-winds and the average annual rainfall of the Los Haitises region is approximately 2000 mm (Zanoni et al. 1990). The wet season extends from May-October. Humidity levels are high and annual average humidity ranges from 70-75% (Zanoni et al. 1990).

Microclimatic variability created by the karst topography and large amounts of precipitation have resulted in one of the highest floral biodiversities in the West Indies with >670 native vascular plant species, 20% of which are Hispaniolan endemics and 32 of these are found only in Los Haitises (Zanoni et al. 1990). The region is particularly rich in orchids (80 species), bromeliads (20 species) and trees (170 species, 14 of which are found only in Los Haitises). Although degraded and fragmented, Los Haitises contains some of the last remaining lowland wet evergreen forest left in Hispaniola, dominated by the emergent hardwoods Balsam Apple *Clusia rosea*, West Indian Mahogany *Swietenia mahogoni*, Silk cotton tree *Ceiba pentandra*, Muskwood *Guarea* *trichilioides*, and endemic palms such as the Royal Palm *Roystonea hispaniolana*. Disturbed areas are dominated by Trumpet tree *Cecropia peltata*.

Similarly, faunal diversity is high, particularly for reptiles and amphibians (Glor et al. 2001). Several species of lizard are endemic to the Los Haitises region (Schwartz and Henderson 1994 cited in Glor et al. 2001). Los Haitises is a critically important site for several threatened bird species, particularly the Hispaniolan Amazon *Amazona ventralis*, White-necked Crow *Corvus leucognaphalus*, and Ridgway's Hawk *Buteo ridgwayi*. Los Haitises National Park is considered an Important Bird Area by BirdLife International (2009), and is also an Alliance for Zero Extinction site (AZE 2010).

The karst primary rainforest of Los Haitises was mainly undisturbed and intact until *c.*1940. In 1967, 208 km^2 of karst forest of Los Haitises was declared a Forest Reserve, and was in turn declared a National Park in 1976, acquiring legal protected status. Although the first human settlements were established within Los Haitises in the 1970's, large-scale environmental damage began in the 1980's with the commercial production of root-crops, primarily several species of Yautia (Taro) *Xanthosoma spp.* and *Colocasia esculenta*, Yuca (Manioc) *Manihot esculenta*, Yame *Dioscorea sativa*, Corn *Zea mays* and Beans *Phaseolus vulgaris* (Marizán 1994). Forest conversion accelerated in the mid-1980s and forest cover decreased by >25% between 1984 and 1989. By 1989 only 10% of the original primary forest remained in the karst region of Los Haitises (Dirección Nacional de Parques et al. 1991). More than 500 families had settled within or near the Park. In 1993, the area encompassed by Los Haitises National Park was expanded from the original 208 km^2 to 1600 km^2.

Nearly all of the remaining vegetation of Los Haitises is a mix of secondary forest, agriculture, pasture and fragmented primary forest The region has been extensively impacted by human activity Logging, cutting for charcoal production, slash-and-burn agriculture, and subsequent conversion to unproductive pastureland and savannah have altered much of the original landscape Most of the remaining forest is limited to the sides and tops of the mogotes, which makes the forest vulnerable to fire The remaining forest is under intense pressure for commercial agriculture of root crops, primarily Yautia, which is in high demand by Dominicans in both the capital of Santo Domingo, and as an export to nationals in the United States Native forest has been replaced over large areas by exotic invasive grasses *Brachiaria spp* , limiting regeneration of native forest (Brothers 1997) Slash-and-burn conversion of forest to root-crop agriculture continues unregulated throughout the Park (Fig 2 3)

2.2.2 Study area

The study site was located on the western side of Los Haitises National Park, and covered an area of *c* 300 km^2 (Fig 2 4) Seven areas within the study site were monitored (Fig 2 5) The study site was centred around the village of Los Limones and was chosen due to the relative accessibility of nesting pairs of Ridgway's Hawk near the village

2.3. GENERAL METHODOLOGIES

2.3.1 Monitoring of breeding pairs and nests

Early-season observations for breeding pairs were made from vantage points on hillsides overlooking valleys to follow movement patterns of adult birds and identify subsequent probable nest locations Weekly visits were made to forest habitats, and activities of territorial pairs were recorded Each valley generally had between *c* 15-25 large trees suitable for nesting. Once adult birds were observed exhibiting nesting behaviour, nests could be located relatively easily Females were vocal during all stages of the breeding episode. They consistently produced loud *Weeup* and Whistle-squeal contact calls (Wiley & Wiley 1981) while at the nest, which made locating active nests relatively easy compared to those of more cryptic species

Once a nest was found, it was visited every 1-3 days (for easily accessible nests), or every 1-2 weeks for sites that were more difficult to access During each visit, the following observations of attending birds and nestlings were recorded during 2-4 hour sessions: nest building activities, brooding and incubation behaviour and duration, food provisioning between mates and to nestlings (including prey species and rates of food delivery), copulations, territorial defense or displays, pair interactions, and nestling interactions and growth Observations were carried out with binoculars and a spotting scope

2.3.2 Trapping, measuring and banding Ridgway's Hawk

Nestlings were accessed at the nest when 25-40 days old. Nestlings were placed in cotton bags and lowered to the ground below the nest, where they were measured, banded, and their blood sampled for DNA. Handling time of nestlings did not exceed 20 minutes per individual.

Adults were captured using bal-chatri noose traps baited with white domestic mice *Mus musculus* (Thorstrom 1996). Adults were not trapped when the pair was incubating eggs.

Morphometric measurements were carried out prior to banding or collection of blood for DNA. Twelve morphological measurements were taken on all birds·

1. *Body mass* : weighed by placing hawks in a cloth bag suspended from a 200g, 300g or 500g Pesola© spring balance;

2. *Wing chord* : unflattened;

3. *Tail length* : measured on the central rectrice from feather shaft base to tip;

4. *Skull length* : from posterior of cranium to base of mandible;

5. *Skull width* : at widest point;

6. *Culmen* : from anterior edge of cere to tip of bill;

7. *Bill depth* : as vertical distance of mandibles at anterior edge of cere;

8. *Bill width* : as horizontal distance of mandibles at anterior edge of cere;

9. *Tarsus length* : from proximal end of intertarsal joint to bend of foot;

10. *Tarsus width* : at the widest point;

11. *Middle toe length* : from proximal joint of basal phalynx to proximal edge of claw;

12. *Middle toe claw* : as chord from proximal to distal extent of claw;

All morphometrics were measured to the nearest 0.1mm, except for wing chord and tail length which were measured to the nearest 1.0 mm, and mass which was measured to the nearest 0.1 gram. Wing and tail rulers were used to measure wing chord and tail length respectively. All other measurements were made using Vernier calipers.

Ridgway's Hawks were banded with colour anodized Acraft© aluminium rivet bands, with internal diameters of 9.5mm for females and 8.5mm for males. The bands were coloured and individually numbered so that different colour combinations could be used to identify individual birds. No more than one band was ever placed on a leg. Color Darvic plastic bands were trialed in 2005 but hawks easily removed them. Nestlings were banded when 25-40 days old.

2.3.3 DNA collection and extraction

Whole blood was collected from 149 Ridgway's Hawks during the study period. Samples were collected from adult, fledgling, and nestling hawks (Table 2.1). Approximately 0.2ml of blood was drawn via capillary tube from a patagial vein puncture, half of which was stored in 1.6ml of Queen's lysis buffer (Seutin et al. 1991) The other 0.1ml of blood was stored in 1.8ml of 95% ethanol. All samples were stored at ambient temperature until delivered to laboratory facilities where they were preserved at –20°C.

Total cell DNA was isolated by blood cell lysis, followed by DNA precipitation using ammonium acetate and isopropanol (L. de Sousa, B. Woolfenden and S. Tarof unpublished protocol for YUMEL). This involved the addition of 50ul of blood/Queen's lysis buffer to 600ul of cell lysis buffer and 5ul of ice cold Proteinase K (40ng/ul). This solution was then incubated at 55-60°C for 5 hours and then at 37°C overnight. Ice cold ammonium acetate (200 ul) was then added, mixed gently, and centrifuged to precipitate protein. The aqueous phase, including the dissolved genomic DNA was removed and placed in a fresh tube. Ice cold isopropanol (600 ul) was added and the solution inverted until DNA was visible as a white floating string or flake. This solution was then centrifuged to collect genomic DNA as a pellet at the bottom of the tube. The supernatant was removed and the DNA pellet washed with ice cold 70% ethanol. This solution was then centrifuged and the ethanol then removed. This ethanol wash was repeated a second time. The tube was then left open and inverted overnight to allow the

DNA pellet to dry completely. The DNA pellet was then suspended in 100-200 ul of TE buffer (10mM Tris-HCl, 1mM EDTA) at 37°C for 24 hours. DNA was stored at 4°C while in use, and at –20°C for longer-term storage.

DNA was visualised under ultraviolet radiation on a 1% agarose test gel, pre-stained with ethidium bromide. Samples were visualised next to a MassRuler high range DNA ladder mix (Fermentas O'GeneRuler^{TM}). Samples were run along with positive (DNA sample of known size) and negative (distilled water) controls.

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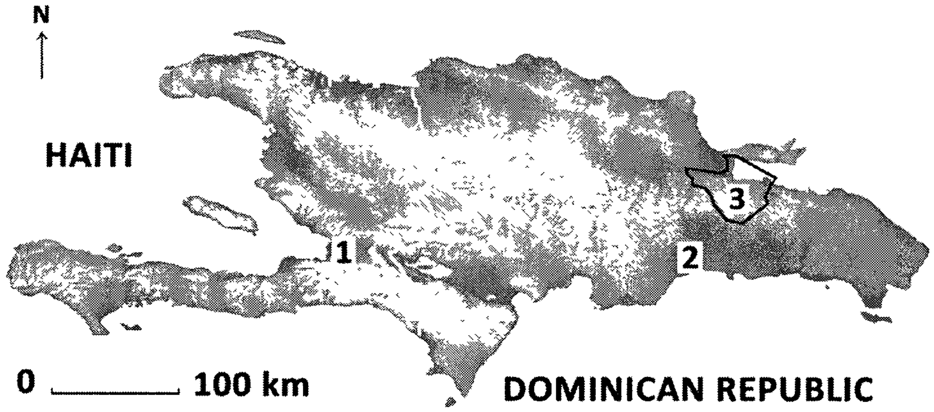

Figure 2.1 Map of Hispaniola showing the locations of : 1. Port-au-Prince; 2. Santo Domingo and; 3. Los Haitises National Park. The National Park boundaries are delineated in black. Image modified from original source at http://earthobservatory.nasa.gov.

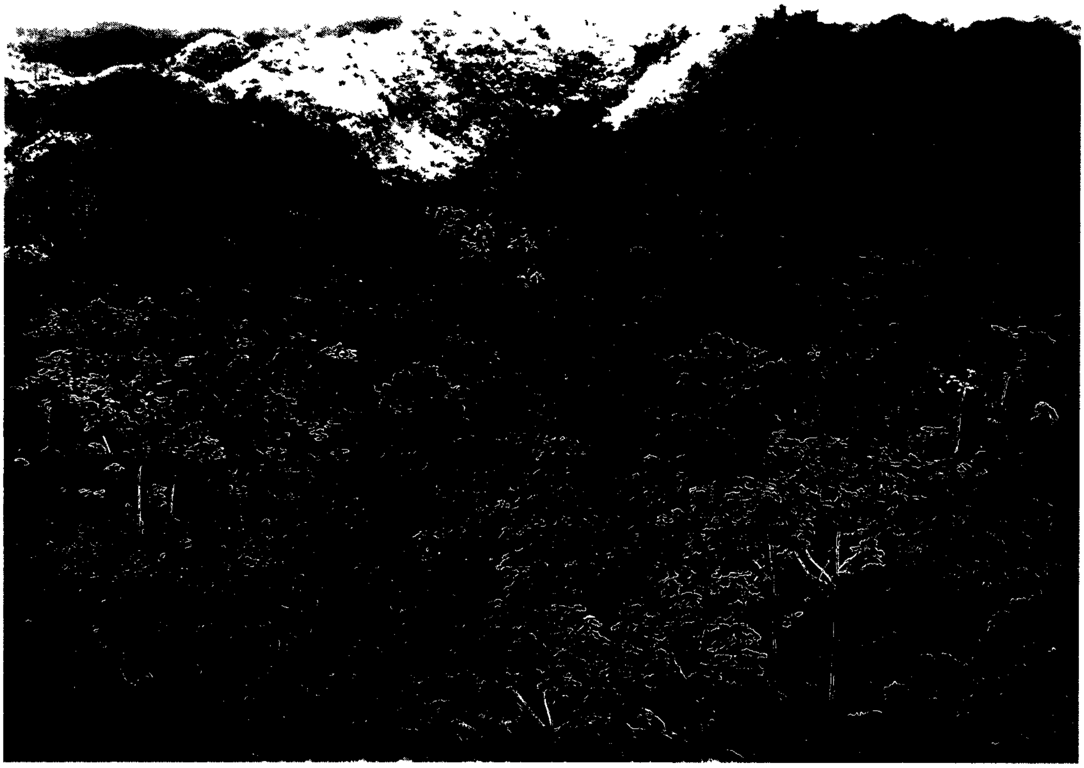

Figure 2.2 Photograph of the karst limestone topography and rainforest of Los Haitises. Photo by Lance Woolaver.

Figure 2.3 Photograph of rainforest illegally burned to clear land for agriculture in 2005, well within the boundary of Los Haitises National Park. There is an active Ridgway's Hawk nest in the nearest palm tree. Photo by Lance Woolaver.

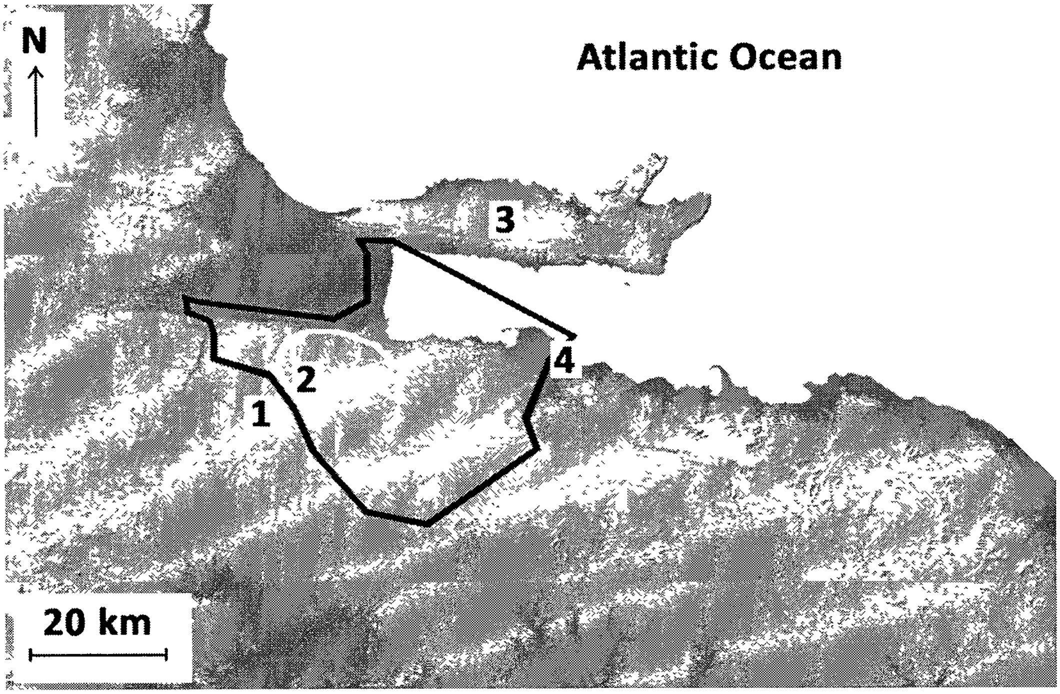

Figure 2.4 Map showing location of : 1. Sabana Grande de Boyá ; 2. Ridgway's Hawk study site within solid white line ; 3. Samaná Peninsula and ; 4. Sabana de la Mar. The boundary of Los Haitises National Park is delineated with a solid black line. Image modified from original source at http://earthobservatory.nasa.gov.

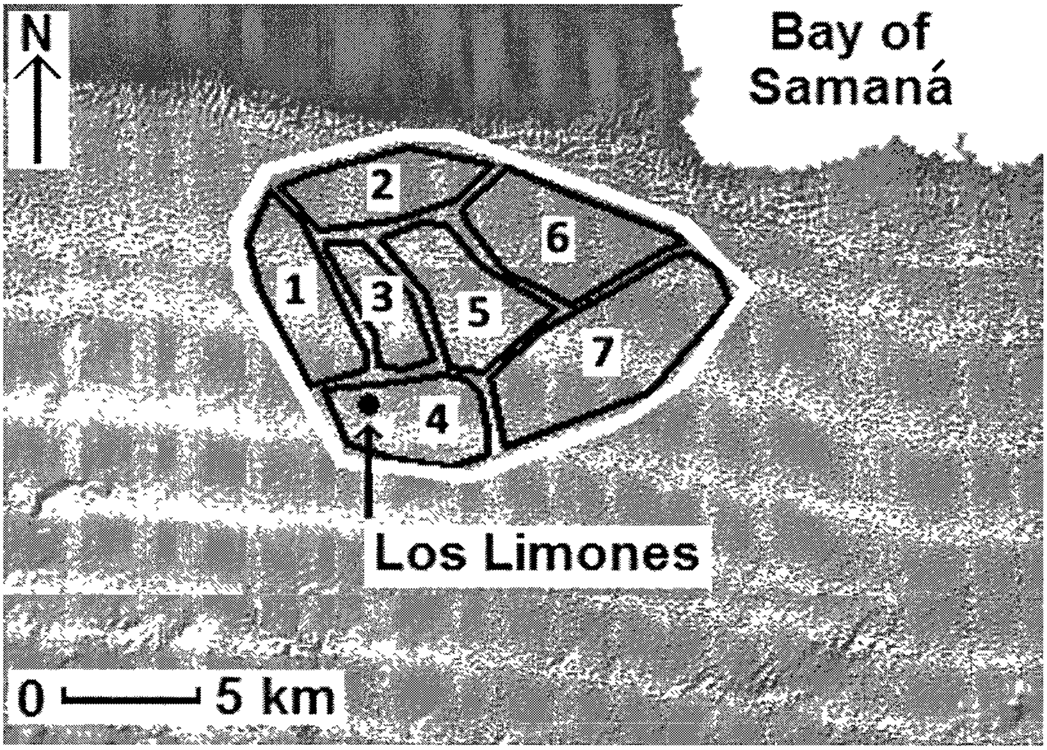

Figure 2.5 Map of the Ridgway's Hawk study site within solid white line. The seven areas surveyed are presented within solid black lines and include : 1. Los Arrollitos ; 2. Cacatona ; 3. Cacata ; 4. Pueblo ; 5. Mata de Limones ; 6. Los Britos and ; 7. Aguatico. Image modified from original source at http://earthobservatory.nasa.gov.

Table 2.1 *Buteo ridgwayi* blood samples collected in Los Haitises from 2005-2008.

	2005	**2006**	**2007**	**2008**	**TOTAL**
Adult	10	11	12	2	35
Fledgling	1	0	1	0	2
Nestling	18	26	29	39	112
TOTAL	29	37	42	41	**149**

Chapter 3

GLOBAL DISTRIBUTION, POPULATION SIZE AND BREEDING DENSITIES

3.1 INTRODUCTION

Ridgway's Hawk was historically found throughout the low elevation coastal forest of Haiti and the Dominican Republic and was relatively common during the 19th century (Appendix 3.1). Although not as frequent, records exist from mid-elevation interior forests. By the end of the 19th century and during the first half of the 20th century, Ridgway's Hawk was considered to be increasingly rare (Peters 1917, Wetmore & Swales 1931) and locally common at only a few sites on offshore islands in Haiti and along the northeastern coast of the Dominican Republic (Bond 1956, Wiley & Wiley 1981). The last record for Haiti was a series of specimens collected from Île à Vache in 1962 (Appendix 3.1) where it was still considered locally common by the collectors (Schwartz & Klinikowski 1965). Ridgway's Hawk is now known from a single declining population in Los Haitises National Park in the northeastern Dominican Republic (Wiley & Wiley 1981, Thorstrom et al. 2005, Thorstrom et al. 2007).

Ridgway's Hawk has been recorded primarily from karst limestone primary forest and secondary forest, and more recently from mixed forest-agricultural plantation (Wiley & Wiley 1981; Thorstrom et al. 2007). Although Ridgway's Hawk has been recorded from 1800m asl (Wiley & Wiley 1981), most records are from lower elevations (<550m asl). Observations of three breeding pairs estimated territory sizes of 47.4, 53.7 and 72.2ha

(Wiley & Wiley 1981) Annual territory re-occupancy rates and turnover rates of established pairs are not known

Ridgway's Hawk is currently listed as Critically Endangered with an estimated global population size of <120 pairs (IUCN 2010a) This chapter reports on the precipitous decline of the species during the last century, briefly examines territory sizes and territory re-occupancy rates, and estimates the current global distribution and population size for the species

3.2 METHODS

3.2.1 Historical and current distribution

Historical distribution for Ridgway's Hawk was determined from a search of the literature, examination of museum specimens, and searches of online museum databases An account of known historical localities is presented in Appendix 3 1 In most cases, localities in the literature and on museum tags were given as place names Location coordinates and elevation were then estimated using Google Earth© Correspondence with collection managers resulted in a compilation of locality information from museum specimens Current global distribution was based on an assessment of remaining available habitat, a compilation of current ornithological knowledge and expert opinion of the island, and visits by the author to potential sites from 2005-2008

3.2.2 Territory size and breeding densities of Ridgway's Hawk in Los Haitises

Methods for finding breeding territories and monitoring nesting pairs are presented in Chapter 2 Breeding territories were defined as areas where the following behaviours indicated the presence of a breeding pair, or a pair that was attempting to breed 1) nest construction, 2) incubation of eggs or brooding of young in the nest, and 3) provisioning of prey items to a nest

All nest GPS locations were plotted on Google Earth For each year, distance between conspecific nests was estimated on Google Earth© (2010) using the ruler tool Only the first nest attempt per breeding pair was used per year The territory size (A) was then calculated as $A = \pi r^2 \times 1\ 158$ where 1 158 was a constant that included the area of non-overlap between adjacent territories (Brown 1975) Radius (r) was half the mean distance to the nearest conspecific nest

Territories were not uniformly spaced throughout the study area Areas of grassland, and burned and/or cultivated areas were unoccupied Therefore, total amount of suitable habitat within Los Haitises was estimated using Google Earth© (2010) This was done by viewing each satellite photo (habitat block) within Los Haitises at an eye altitude of ~1 km, and estimating the amount of forest covered habitat remaining for each block This was done within the full 1600km^2 area

Annual breeding densities were estimated on Google Earth© by plotting a polygon that enclosed all nests within the survey area, and then calculated as the number of territories per 100km^2 Assuming equal habitat suitability within studied and unstudied areas, annual breeding densities were extrapolated to the amount of similar habitat within the total area of the National Park, for a total estimate of number of breeding pairs in Los Haitises per annum The global population estimate (with a minimum to maximum range) was then calculated using the average breeding density over the study period, with an estimated 3-7% annual habitat loss within the Park (see Section 3 3 2)

3.3 RESULTS

3.3.1 Historical and current distribution

Ridgway's Hawk records and museum specimens from Haiti are primarily from the satellite islands of Petite and Grande Cayemite, Île à Vache and Île de la Gonâve. There are two records from the mainland of Haiti, one from the western coast near Geffard (Wiley & Wiley 1981) and the other from Bois Laurence in the Massif du Nord, where Bond recorded two nest attempts and collected a female specimen in 1928. All but the Bois Laurence records were from <556m asl. The exact location of the Bois Laurence records and specimen are not reported but the Massif du Nord ranges in elevation from 360-1024m asl. Ridgway's Hawk was becoming increasingly rare in Haiti during the early 20th century (Wetmore & Swales 1931) but was still considered locally common on Grande Cayemite in the early 1900s (Abbott in Wetmore & Swales 1931), and on Île à Vache in 1962 (Schwartz & Klinikowski 1965). A series of specimens (4 males and 2 females) were collected from Île à Vache on August 4, 1962. This is the last record for the species in Haiti (Keith et al 2003). No Ridgway's Hawks were recorded during avifaunal surveys of Île de la Gonave in 1985 (M.A. MacDonald in litt. 1991 cited in Collar et al. 1992) or Île à Vache in January of 2000 (Brooks & Davalos 2001).

There are records for Ridgway's Hawk from the western Dominican Republic. Ridgway's Hawk was recorded on the satellite island of Isla Beata in May of 1931 by Wetmore & Lincoln (1934). No Ridgway's Hawks were recorded on Isla Beata during intensive avifaunal surveys in May of 1974 (Faaborg 1980) or July of 1977 and October of 1978 (Wiley & Ottenwalder 1990). Wiley observed an individual Ridgway's Hawk on the nearby small islet of Alto Velo on October 22, 1978. The hawk was perched in the tallest vegetation and flying over Sooty Tern *Onychoprian fuscata* colonies (Wiley & Ottenwalder 1990).

Dod (1978) recounts a close observation of a Ridgway's Hawk at Angel Felix, north of the Sierra de Bahorucos, and describes the nearby area of La Descubierta as a site where the species was locally common until the forest was cleared. These areas were at moderate elevations ranging from 420-1100m asl. Dod (1978) and Wiley & Wiley (1981) report several other localities in the western Dominican Republic (Casavito, Rancho Francisco, San José de Ocoa) although details of any sightings, and exact details of the locations are not provided.

There is a brief mention of Ridgway's Hawk being observed at 1800m asl at Valle Nuevo (Wiley & Wiley 1981) but no details are provided as to the date, number of hawks, habitat type or behaviour of the Hawk(s) at that site.

There are two reliable sightings of Ridgway's Hawk on the southern coast of the Dominican Republic near Haina and Santo Domingo (Danforth 1929).

By far the majority of museum specimens and historical records are from the eastern and northeastern coast of the Dominican Republic, and are associated with karst lowland rainforest at elevations <327m asl. Wetmore & Swales (1931) describe Ridgway's Hawk as a "species of the lowlands". Cory (1885) describes Ridgway's Hawk as "not uncommon in the valley of the Yuma River, but is nowhere abundant."

During the 1990s the species was considered to be near extinction with nearly all known historical localities extirpated or available forest habitat destroyed. Only a few pairs were known from Los Haitises National Park (Nigel Collar in litt. 2004). Surveys in 2002-2003 by Thorstrom et al. (2005) and the author in 2004 documented that a small population remained within the park.

The most recent reliable sightings outside of Los Haitises National Park were made by Miguel Angel Landestoy, Pablo Weaver, and Arlen Maremolejo on July 12, 2003 on the Samaná Peninsula (P. Weaver in litt. 2004, see Appendix 3.1 for details). Individual Ridgway's Hawks were either heard or seen near the village of Samaná and 13km to the east near Salta de Limon. It is unclear whether these are remnant birds from when the region was covered in larger areas of forest or whether these were birds that had dispersed from Los Haitises, 22km to the south.

No other areas were found outside of Los Haitises with Ridgway's Hawks during the study period 2005-2008. However, the author did not visit Isla Beata in the southwest of the Dominican Republic, or the Samaná Peninsula north of Los Haitises, two areas that may still harbor a small number of pairs. Avifaunal surveys by the author to Loma Quita Espuela along the northern coast in April of 2004, and to the Cordillera Oriental between El Seibo and Miches in April of 2006 (see Appendix 3.1) revealed no Ridgway's Hawks. Interviews with local people confirmed that Ridgway's Hawks were known to some of the older villagers in the Cordillera Oriental, and had been locally common when more forest existed in the region 10 years previously. One man stated that he had last seen a Ridgway's Hawk in the area near the top of the Cordillera in 2003.

The historical range for Ridgway's Hawk included the island of Hispaniola and its satellite islands, encompassing an area of 78,442 km^2. The present study found the Hawk restricted to an area of *c.*1,600 km^2 within Los Haitises National Park. If the extent of occurrence includes the 2003 sightings on the Samaná Peninsula, an area of *c.*1,050 km^2, the total global range of the species or 'extent of occurrence' as classified by the IUCN (2010b) is estimated at 2,650 km^2. This represents a >96% decrease in the species range. The actual 'area of occupancy' (IUCN 2010b) for the species is likely < 500 km^2.

3.3.2 Territory size and breeding densities in Los Haitises National Park

Los Haitises National Park covers an area of *c.*1,600 km^2. However, the total amount of habitat within the Park suitable for breeding hawks was estimated to be approximately 950km^2, based on visiting different areas of the Park and using satellite imagery from Google Earth©. This estimate was calculated from satellite photos taken between 2003-2006, and consequently would represent the maximum amount of suitable habitat still available. Habitat loss within the study area has continued unabated since 2006 (author pers. obs; T. Hernandez pers. comm.). Therefore breeding pair estimates for 2005 and 2006 were calculated within an area of 950 km^2, but from 2007-2009 the breeding pair estimates were calculated with a 5% annual loss of habitat. This amount was chosen as the average of the estimated 3-7% habitat loss per year noted during the study period, and is also consistent with other estimates of forest loss within Los Haitises National Park determined from satellite photos (Brothers 1997a, 1997b). The estimates for numbers of breeding pairs in 2007 were calculated with an area of suitable habitat of 902.5 km^2, 2008 estimates with an area of 857.4 km^2, and 2009 estimates with an area of 814.5 km^2.

Distance to nearest conspecific nest for all nesting territories monitored during the study period averaged 607 ± 276m and ranged from 199-1197 m (n=140). Mean distance to nearest conspecific nest did not differ significantly among years ($F_{4,135} = 0.45$, $p = 0.48$).

Over the study period, territory sizes averaged 33.2 ± 7.1 ha (Table 3.1). Annual breeding density estimates ranged from 10.5 to 13.8 pairs per 100 km^2 and averaged 12.6 pairs per 100 km^2 over the study period (Table 3.1).

3.3.3 Territory re-occupancy rates

Annual territory re-occupancy rates ranged from 91.1 to 100% and averaged 94.5 ± 3.9% over the study period. Due to the limited number of banded adults, it was not possible in the majority of cases to determine if the same full pairings were returning or not. Nevertheless, there were clear traditional territories used by this species over the study period.

Sightings of banded birds did suggest that established adults were returning to the same territories. Two banded adult males returned to the same territories each year over the 5-year study period. It is unknown if they had the same mates throughout the study as their females were not banded. Of four banded pairs that could be followed from 2005-2009, one pair held a territory for the 5-year study period, and one pair was replaced after 3 years. In the remaining two pairs, the females were replaced after 1 and 2 years, respectively. Three females and three males held the same territory during the full period of time for which they were monitored throughout the study; but they were not followed for longer than 3 consecutive years. There were also five additional observations of mate replacement over the study period from birds monitored ≤ 3 years. The banding data suggests that pair replacement (turnover rate) was quite high, although the sample size was small.

3.3.4 Total population estimate

Total number of estimated breeding pairs in Los Haitises National Park ranged from 99 to 131 annually and averaged 112 ± 13 breeding pairs (Table 3.1). The annual estimates suggest a decrease in number of breeding pairs from 131 pairs in 2006 to 103 pairs in 2009. If this similar rate of decline continues unabated (21% decline over 4 years), the maximum time to extinction for the species, without any other compounding factors, would be 2 decades.

The current global population estimate of Ridgway's Hawk is 91 to 109 breeding pairs, all within Los Haitises National Park. This is based on a mean breeding density of 12.6 pairs per 100km^2 and two potential habitat loss scenarios: a conservative estimate of 3% annual habitat loss and a more liberal estimate of 7%.

3.4 DISCUSSION

3.4.1 Territory size and re-occupancy

The average breeding territory size of Ridgway's Hawks (33 ha) was similar to that of the geographically closest forest *Buteo*, the Puerto Rican Broad-winged Hawk *B. platypterus brunnescens* which has an average territory size of 39.5 ha (Delannoy & Tossas 2000). Both inhabit similar karst forest habitats (Monroe 1968). The present study supports previous research documenting reduced space requirements for tropical raptors when compared to their temperate mainland counterparts. Territory sizes of *B. ridgwayi* are substantially smaller than temperate populations of the Red-shouldered Hawk *Buteo lineatus,* its closest taxonomic relative. *B. lineatus* home ranges vary from 100-200 ha (Dykstra et al. 2008), compared to the mean of 33.2 ± 7.1 ha for *B. ridgwayi.* Similarly, nesting territories observed for the Puerto Rican Broad-winged Hawk were *c.*8

times smaller than the mainland subspecies (Keran 1978, Delannoy & Tossas 2000). Gannon et al. (1993) found that Puerto Rican Screech-Owl *Otus nudipes* home ranges were smaller than ranges of similar-sized temperate owls by a factor of ten or more.

The mean distance of 607 ± 276m between Ridgway's Hawk nests for the present study was less than the 727m ± 374m reported for Ridgway's Hawk by Wiley & Wiley (1981), and significantly less than the 1.27 ± 0.64 km reported by Crocoll & Parker (1989) for *Buteo lineatus*.

The relatively small territory sizes and close nesting proximity of breeding pairs in Los Haitises is due in part to the topographic features and productivity of the landscape. Haystack hills (*mogotes*) and valleys may provide increased opportunities for exchanging visual cues and auditory cues between adjacent pairs, thereby reducing conspecific competition and pressure on territorial behavior. More likely, the steep hills and valleys create vertical habitat for hunting, which is not represented in the two-dimensional estimates of territory sizes. The *mogotes* in Los Haitises are refuges for a high abundance and diversity of reptile species (Glor et al. 2001), which form the main prey base of Ridgway's Hawk (Chapter 5). Raptor space requirements can be regulated by competitor abundance and prey abundance (Dunk & Cooper 1994), both of which are optimized by the karst topography of Los Haitises. This karst topography is likely one of the main reasons that Ridgway's Hawk have been able to persist in relatively high densities within the small remaining fragmented forest of Los Haitises.

Nearly all nesting territories monitored over consecutive years were re-occupied. This high re-occupancy rate suggests that these are traditionally used territories. High re-occupancy rates were also documented in the endangered Puerto Rican Sharp-shinned

Hawk *Accipiter striatus venator* (Delannoy & Cruz 1988) and the Puerto Rican Broad-winged Hawk (Hengstenberg & Vilella 2005). Threatened species that are limited by specific habitat requirements, like forest raptors, and that are suffering from widespread habitat loss would be expected to place a high premium on all remaining habitat, and it is not unexpected that traditional territories for Ridgway's Hawk would have a high re-occupancy rate.

It was not possible to determine in most cases if the same pairs re-occupied a territory in consecutive years, but observations of banded bird sightings did suggest high nest site fidelity. However, banding data also suggested a high rate of mate replacement which is a cause for concern in this small population. A high turnover rate in this population is most likely due to adult mortality and not divorce, since *Buteo* species generally exhibit long-term pair bonds with a very low rate of divorce (Newton 1979). In support of this, banded birds that were replaced were not re-sighted at all in subsequent years in other areas. Of the four banded pairs followed over the 5-year period, one pair remained together on a territory in an area where the landowner protected the hawks from human persecution. The remaining three territories where individual birds were replaced were within areas where landowners were known to persecute the hawks.

3.4.2 Global distribution, population size and trend

Historical stronghold areas for Ridgway's Hawk outside of the northeastern Dominican Republic were the larger offshore islands of Haiti: Île à Vache, Île de la Gonâve, and the Cayemites (Wetmore 1932, Wetmore & Lincoln 1934, Schwartz & Klinikowski 1965); the low elevation forest near Santo Domingo (Danforth 1929) and the mid elevation forest near Lago Enriquillo (Dod 1978). Large scale forest clearance at these sites has resulted in the extirpation of Ridgway's Hawk from all of them. Aerial surveys of the off-shore islands of Haiti by J. A. Ottenwalder (in litt. 1992, cited in Collar et al. 1992) found that with the exception of Grande Cayemite all of the other satellite islands of Haiti were either heavily disturbed and/or densely populated. Satellite photos of Grande Cayemite from July 5, 2009 confirm that the remaining forest cover is heavily fragmented by slash-and-burn agriculture.

The extent of occurrence for Ridgway's Hawk has decreased precipitously, by at least 96% during the last century or so. The remaining global population appears to be limited to Los Haitises National Park. There is the small possibility that a few pairs could still persist on Isla Beata in the southwest, and/or within small patches of riparian forest on the Samaná Peninsula or near Arroyos Santiago on the Cordillera Oriental. However, these populations would be so small and isolated as to not be viable over any period of time. Wiley & Wiley (1981) found birds persisting in the degraded wet forest above Miches on the northern coast of the Dominican Republic in the mid-late 1970s, but did not find any birds in "the largely destroyed forests of the Samaná Peninsula" during that same time period. At best, the remaining small fragments of forest on the Samaná Peninsula could only support 2-4 breeding pairs. The highly fragmented forests (<38.72 km^2) on the northern slope of the Cordillera Oriental above Miches would only be able to support a few breeding pairs. All suitable nesting habitat in Los Haitises is saturated (author pers. obs.), and young birds not able to acquire optimal habitat or traditional territories are likely dispersing into the surrounding areas outside of the Park to look for available habitat, but none is available.

It is extremely unlikely that any Ridgway's Hawks remain in Haiti, or that any viable populations exist outside of the remaining karst rainforest of Los Haitises in the northeastern Dominican Republic.

3.4.3 Conservation implications

Ridgway's Hawk is classified as 'Critically Endangered' by the IUCN (2010a) on the basis of the following criteria:

1. A population size of fewer than 250 mature individuals,
2. An inferred continued decline in the number of mature individuals and,
3. At least 90% of mature individuals in one subpopulation.

Ridgway's Hawk has been extirpated from >96% of its original extent of occurrence during the last century. The world population of Ridgway's Hawk is between 182-218 adult individuals and the entire breeding population of adults is restricted to one locality in Los Haitises National Park. A continual decline of this population can be inferred from the decrease in pairs observed in Los Haitises National Park over the study period (131 pairs in 2006 to 103 pairs in 2009). The low estimate of 99 pairs in 2005 is likely due to that year being a preliminary field season and the lack of experience with the study species and study area.

An even greater decline of the population can be expected in the near future, as neither the continuous conversion of forest to slash-and-burn agriculture nor the human persecution of hawks have diminished (Chapter 4). Although active persecution of the hawks decreased somewhat during the study period due to community based efforts to protect hawk nests instigated by international conservation NGOs, the unsustainable rate of slash-and burn agriculture increased. Los Haitises National Park is unfortunately a "paper park" with poorly defined and shifting borders, and no local enforcement or government regulation (author pers. obs., Geisler et al. 1997). The presence of the last remaining population of Ridgway's Hawk within Los Haitises National Park does not guarantee the protected status of the species' and its habitat (Latta et al. 2006). In fact, one could argue the opposite and that the Hawk would be more secure on private lands where unregulated slash-and-burn by migrant human populations would not be so pervasive. The future survival of Ridgway's Hawk in its natural environment very much depends on the effective management and protection of Los Haitises National Park.

The current distribution, size, structure and rapidly declining trend of the remaining population of Ridgway's Hawk clearly warrants a 'Critically Endangered' listing for the species. The use of traditional territories with high re-occupancy rates, the dependence on forest cover and associated prey base, and the need for an area free of human persecution have made this species vulnerable to habitat conversion and destruction throughout its range during the last century. If human persecution and forest destruction continues unregulated within the last stronghold area of Los Haitises, the species will become extirpated from its natural environment.

The estimated population size for Ridgway's Hawk is extremely low for a top-level predatory vertebrate, and the minimum viable population size has not yet been modelled for this species. Ridgway's Hawk may be approaching a threshold where a combination of environmental, demographic and genetic factors interact and force the species into an extinction vortex (Gilpin & Soulé 1986). An analysis of ten true species extinctions, including five avian species (Fagan & Holmes 2006), found that on average, final declines to extinction started from 70 (± 39) individuals, with three populations declining directly from > 100 individuals. Ridgway's Hawk, with a low population estimate of 182 adults, could already be extremely close to the minimum viable population size for the species.

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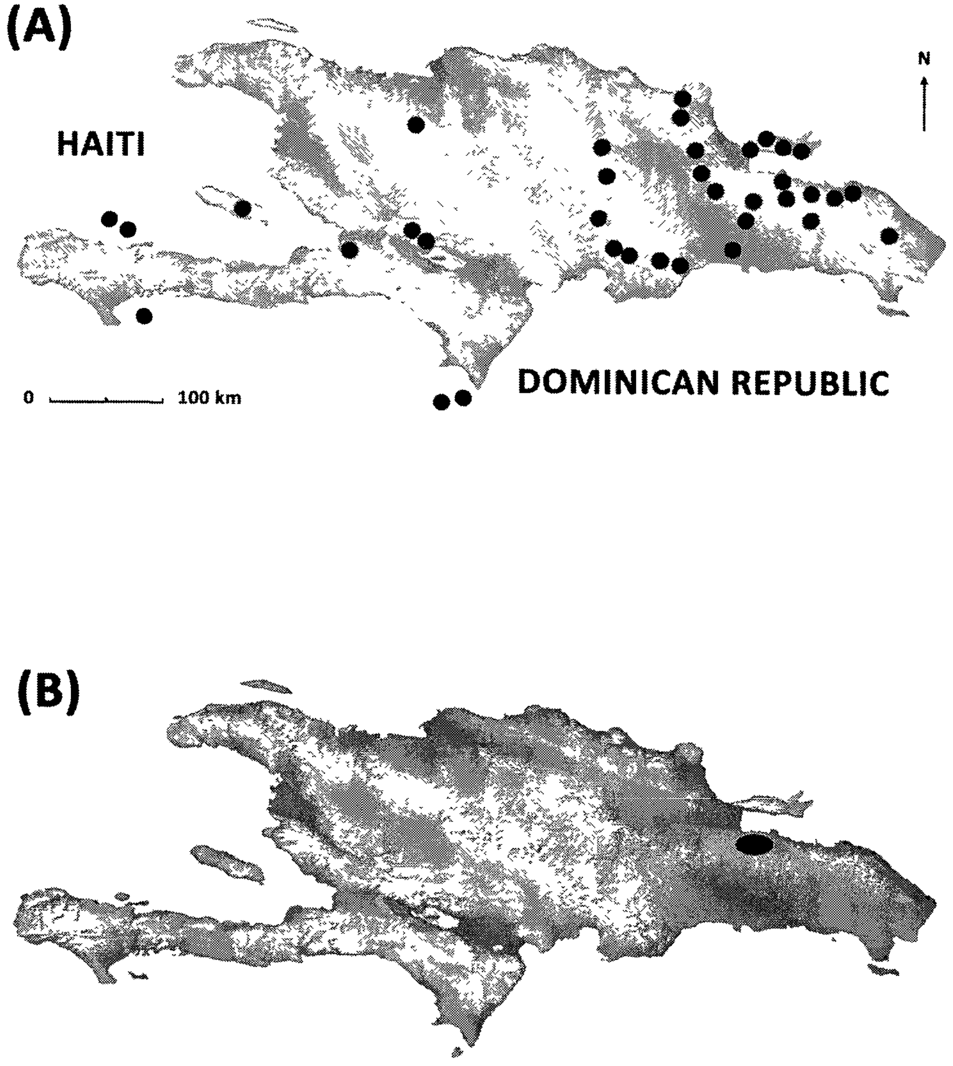


Figure 3.1 Map of Hispaniola showing : (A) historical localities and (B) known remaining population locality of Ridgway's Hawk. Image modified from original source at http://earthobservatory.nasa.gov. See Appendix 3.1 for detailed information on historical sites.

Table 3.1 Annual estimates of territory size, breeding density, and total number of breeding pairs of Ridgway's Hawk within Los Haitises National Park, 2005-2009.

Year	Number of pairs monitored (n)	Nearest nest distance Mean ± SD (range) in meters	Territory size Mean ± SD in ha	Breeding density [a] (# of pairs / 100km^2)	Number of breeding pairs in Los Haitises [b]
2005	16	667 ± 372 (199 - 1172)	40.4 ± 12.5	19 / 180km^2 (10.5 / 100km^2)	99
2006	31	603 ± 265 (241 - 1054)	33.1 ± 6.4	34 / 245km^2 (13.8 / 100km^2)	131
2007	39	549 ± 251 (205 - 1082)	25.0 ± 5.7	41 / 300km^2 (13.2 / 100km^2)	119
2008	25	574 ± 258 (241 - 1197)	30.5 ± 6.1	28 / 225km^2 (12.4 / 100km^2)	106
2009	32	645 ± 232 (280 - 1051)	37.8 ± 4.9	35 / 275km^2 (12.7 / 100km^2)	103
Total Range		**199 - 1197**	**25.0 – 40.4**	**10.5 - 13.8 pairs / 100 km^2**	**99 - 131**
Total Mean		**607 ± 276**	**33.2 ± 7.1**	**12.6 ± 1.3 pairs / 100 km^2**	**112 ± 13**

[a] Annual breeding density, calculated as number of territories observed per area surveyed per annum.

[b] Breeding pairs estimate within Los Haitises National Park, calculated as the breeding densities per area of available habitat (See Section 3.3.2).

Table 3.2 Territory re-occupancy rates of Ridgway's Hawk in Los Haitises National Park, 2005-2009.

Year	Number of Territories	Proportion used from previous years	Percent of territories re-occupied
2005	19	-	-
2006	34	19/19	100%
2007	41	31/34	91.1%
2008	28	26/28	92.8%
2009	35	33/35	94.2%
			Mean 94.5 ± 3.9%

APPENDIX 3.1 Description and map of Ridgway's Hawk historical localities based on literature and museum specimens

Ridgway's Hawk was historically found in low coastal karst rainforest and mid-elevation transitional forest throughout Haiti and the Dominican Republic but has disappeared throughout most of the historical range, primarily due to loss of forest to slash-and-burn agriculture and to direct human persecution. It is most definitely extirpated in Haiti. Historical localities, based on the literature and on museum specimens, are presented in Figure 1. Accounts from Threatened Birds of the Americas (Collar et al. 1992) provided an invaluable starting point for tracking down historical information for many localities, particularly for Haiti. Jim Wiley's *A Bibliography of Ornithology in the West Indies* (2000) was also useful in searching for literature references and museum specimens.

1-Isle Petite Cayemite, Haiti (18°36'49.06"N 73°48'36.57"W). Ridgway's Hawk was common on the island in the early 1900s according to Abbott (Wetmore & Swales 1931, Wiley & Wiley 1981). An adult male collected by Abbott on January 13, 1918 is stored at the National Museum of Natural History, Washington DC. Petite Cayemite is only 0.65km by 1km and 0-63m asl.

2-Isle Grande Cayemite, Haiti (18°37'23.20"N 73°44'36.35"W). This was an historical Ridgway's Hawk locality as cited in Dod (1978). Ridgway's Hawk was common on the island in the early 1900s according to Abbott (Wetmore & Swales 1931, Wiley & Wiley 1981). A series of specimens (7 males, 6 females) collected from Grande Anse by Abbott from January 6-18, 1918 are stored at the USNM, the MCZ, and the AMNH. Grande Cayemite is 9.8km by 6.4km, ranging in elevation from 0-116m asl.

3-Île à Vache, Haiti (18°04'39 20"N 73°36'13 08"W) Ridgway's Hawk was common on the island in 1962 (Schwartz & Klinikowski 1965) Two males and a female collected on the western end of the island by Parish & Perry on April 30, 1930 are stored at the USNM An adult male collected by the same collectors from the north-central part of the island on May 1st, 1930 is also stored at the USNM An adult female collected on the island by Wetmore & Swales on April 28, 1931 is stored at the USNM Four males and a female collected by Klinikowski, Schwartz & Rigaud from the western end of Île à Vache on August 4, 1962 are stored at the Museum of Natural Science, Louisiana State University, Baton Rouge A male collected by Paulson from the western end of Île à Vache on August 4, 1962 is stored at the Museum of Zoology, University of Michigan, Ann Arbor Ridgway's Hawk was not seen during an avifaunal survey of the island in January of 2000 (Brooks & Davalos 2001) Île à Vache is 11km by 4 5km with an elevation range of 0-24m asl The island is 16km from the main island of Hispaniola

4-Île de la Gonâve, Haiti (18°48'53 42"N 72°58'33 28"W) Three Ridgway's Hawks were recorded circling together over lowland forest on July 18, 1927 by Danforth (Danforth 1929) No Ridgway's were seen in February 1985 (M A McDonald in litt 1991 in Collar et al 1992) This is a large island of 57km by 12km with an elevation range of 0-556m asl The island is 21km from the main island of Hispaniola

5-Geffard, Haiti (18°31'14 91"N 72°35'26 61"W) This was an historical Ridgway's Hawk locality as cited in Wiley & Wiley (1981) Elevations in the area range from 40-70m asl

6-Bois Laurence, Massif du Nord, Haiti (19°16'48 86"N 71°55'29 05"W) Two Ridgway's Hawk nests were recorded with white down covered nestlings by Bond on May 2, 1928 One nest was 7 6m above ground, the other 12 2m above ground (Dod 1978, Wiley & Wiley 1981) A female collected by Bond at Bois Lawrence on May 2, 1928 is stored at the Academy of Natural Sciences, Philadelphia (ANSP) Elevation in the region ranges from 360-1024m asl There is no forest left

7-Angel Felix, DR (18°38'33 23"N 71°46'17 05"W) A Ridgway's Hawk was observed near Angel Felix by Dod (1978) The Hawk was on a low perch in a tree near the road and was observed for 15 minutes The Hawk had a full crop, and was preening and gaping slightly Elevation along the road near Angel Felix ranges from 490-1022m asl There is very little forest left in the area

8-La Descubierta, DR (18°34'22 74"N 71°44'30 65"W) This was cited by Dod (1978) as a site where Ridgway's Hawk was still found in the 1970s Elevation in the area ranges from 65-840m asl The forest has subsequently been cleared There are still fragmented forest patches (6km by 8km) on the mountainside at 420-840m asl to the north of La Descubierta that could support 3-5 pairs

9-Isla Alto Velo, DR (17°28'37 51"N 71°38'26 92"W) A single Ridgway's Hawk was seen on the NW part of the island perched in the highest part of the vegetation, and soaring over a Sooty Tern colony on October 22, 1978 (Wiley & Ottenwalder 1990) The island is small at 1 1km by 1 4km Elevation ranges from 0-128m asl the island still possesses some subtropical dry forest cover Alto Velo is 12km from Isla Beata

10-Isla Beata, DR (17°34'54 47"N 71°31'20 74"W) Ridgway's Hawk was recorded on Isla Beata by Wetmore & Lincoln (1934) No Ridgway's Hawks were recorded on Isla Beata in May 1974 (Faaborg 1980) or July 1977 and October 1978 (Wiley & Ottenwalder 1990) A Ridgway's Hawk was seen on nearby Alto Velo by Wiley & Ottenwalder (1990) in October 1978 and it is possible that this individual came from Isla Beata or the main island of Hispaniola The forest on Isla Beata has not changed during the last century and there have been relatively low levels of human impact on the island No one lives on the island permanently It is possible that a small population of Ridgway's Hawk (<6 pairs) persists on the island The island is 8km by 6km and ranges in elevation from 0-79m asl Isla Beata is 5 25km from the main island of Hispaniola

11-La Vega, DR (19°12'51 97"N 70°33'10 29"W) This was an historical Ridgway's Hawk locality as cited in Wiley & Wiley (1981), possibly based on Verrill & Verrill (1909) Elevation in the area ranges from *c* 195-550m asl, along the base of the eastern slope of the Cordillera Central Some karst rainforest remains on the eastern slope of the Cordillera Central, west of the road between La Vega and Miranda between 300-550m asl which could support <6 pairs

12-Casavito, DR (19°02'0 00"N 70°30'60 00"W) There was an historical Ridgway's Hawk locality called Casavito in Dod (1978) It is not clear but this could be Casabito near Ebano Verde Scientific Reserve The area is at a fairly high elevation ranging from 1160-1432m asl There is no forest left

13-Rancho Francisco, DR (18°30'5 09"N 70°29'26 91"W) This was an historical Ridgway's Hawk locality as cited in Wiley & Wiley (1981) Elevation in the area ranges from 505-769m asl There is no forest left

14-Valle Nuevo, DR (18°53'37 23"N 70°45'34 39"W) Ridgway's Hawk has been recorded by James Wiley at 1800m asl in Valle Nuevo (Wiley & Wiley 1981) Elevation in the area ranges from 1153-2224m asl There is a small patch of forest remaining in a scientific reserve of c 10km by 3km

15-San José de Ocoa, DR (18°32'50 07"N 70°30'53 03"W) This was an historical Ridgway's Hawk locality as cited in Dod (1978) and Wiley & Wiley (1981) Elevation ranges from 472-734m asl There is a small patch of forest 3 4km by 4 1km on the western slope near the town

16-Cambita, DR (18°27'0 83"N 70°12'12 97"W) This was an historical Ridgway's Hawk locality as cited in Wiley & Wiley (1981) Dod (1978) mentions an area called La Colonia de

Cambita but it is unclear whether these are the same localities Elevation ranges from 176-309m asl There are only fragments of forest left

17-Haina, DR (18°25'03 83"N 70°01'43 19"W) A single Ridgway's Hawk was sighted by Danforth on June 16, 1927 (Danforth 1929) Elevation ranges from 9-69m asl There is no forest left

18-Santo Domingo, DR (18°34'24 73"N 69°44'31 46"W) An individual Ridgway's Hawk was seen by Danforth on July 4 and 8, 1927 (Danforth 1929) Elevation ranges from 15-28m asl There is no forest left

19-Bayaguana, DR (18°45'48 47"N 69°37'46 62"W) This was an historical Ridgway's Hawk locality as cited in Wiley & Wiley (1981) Elevation ranges from 32-67m asl There is no forest left

20-Hato Mayor, DR (18°45'54 88"N 69°14'55 62"W) This was an historical Ridgway's Hawk locality as cited in Wiley & Wiley (1981) Elevation ranges from 98-272m asl There is no forest left

21-Higuey, DR (18°37'39 43"N 68°42'04 51"W) This was an historical Ridgway's Hawk locality as cited in Wiley & Wiley (1981) Elevation ranges from 88-107m asl There is no forest left

22-Guarabo / La Cuchoreta, DR (18°59'30 01"N 68°56'20 92"W) This was an historical Ridgway's Hawk locality as cited in Wiley & Wiley (1981) A male collected at Guarabo, near Jovero by Abbott on November 18, 1923 is stored at the National Museum of Natural History, Washington DC Elevation ranges from 42-114m asl There is no forest left

23-Miches, DR (18°58'25 16"N 69°02'26 93"W) This was an historical Ridgway's Hawk locality as cited in Wiley & Wiley (1981) Elevation ranges from 8-142m asl There are fragmented areas above Miches on the northern slope of the Cordillera Oriental totalling *c* 38 72km^2

24-Loma La Herradura, DR (c 18°54'27 36"N 69°06'37 71"W) This is an area reported by Timoteo Hernandez to potentially still have Ridgway's Hawk, or at least to have some intact forest left Elevation ranges from 89-570m The largest available patch of intact forest is *c* 152km^2 Four juveniles were translocated by The Peregrine Fund and Sociedad Ornitólogica Hispaniola to a private reserve owned by Centro Romano in 2008

25-Magua, DR (18°58'60 00"N 69°13'60 00"W) This was an historical Ridgway's Hawk locality as cited in Wiley & Wiley (1981) as Seibo / Magua but the locality on the map does not correspond to the towns of Seibo and Magua A female Ridgway's Hawk collected by Cory on January 31, 1883 (Cory 1883) is stored at the Field Museum of Natural History (FMNH), Chicago Elevation ranges from 12-287m asl

26-El Seibo, DR (19°01'16 22"N 69°23'20 93"W) Two Ridgway's Hawks (a male and an unknown) collected by Klimikowski & Schwartz on January 18 and 22, 1963 are stored at the Museum of Natural Science, Louisiana State University, Baton Rouge The location name was given as El Seibo, 3 5 miles south of Sabana de la Mar The location is likely correct but El Seibo is 30+ km to the southeast of Sabana de la Mar Elevation near El Seibo ranges from 17-133m asl On April 5, 2006 Lance Woolaver, Timoteo Hernandez and Jorge Brocca drove across the Cordillera Oriental from El Seibo to Miches There was very little existing forest left One man we questioned at the top of the Cordillera near some remnant forest in the valleys said that 10 years ago there was still a large amount of forest and both Ridgway's Hawk and Red-tailed Hawk were locally common, but he hadn't seen a Ridgway's Hawk for the last 3 years We observed a juvenile RTHA near this man's house

27-Sabana de la Mar, DR (19°04'02 06"N 69°23'26 29"W) This was an historical Ridgway's Hawk locality as cited in Wiley & Wiley (1981) Elevation ranges from 0-7m asl

28-Arroyon, DR (18°57'16 68"N 69°29'27 50"W) This was an historical Ridgway's Hawk locality as cited in Wiley & Wiley (1981) Eastern Los Haitises is mentioned as a locality by Dod (1978) Elevation ranges from 198-285m asl

29-Pilancón / Vereda, DR (18°54'24 41"N 69°34'45 79"W) This was James Wiley's study site where 3 pairs were monitored in 1976 (Wiley & Wiley 1981) Elevation ranges from 203-295m asl

30-Sabana Grande de Boyá / Zapoté, DR (18°56'58 35"N 69°47'32 43"W) This was an historical Ridgway's Hawk locality as cited in Wiley & Wiley (1981) Elevation ranges from 210-295m asl

31-Miranda, DR (19°01'05 50"N 69°53'12 21"W) This was an historical Ridgway's Hawk locality as cited in Wiley & Wiley (1981) A nearby area called Los Ojos de Aras, is reported as possibly having some intact forest and Ridgway's Hawks by Timoteo Hernandez Elevation ranges from 54-221m asl

32-Villa Riva / Almercen, DR (19°10'53 71"N 69°54'01 17"W) A pair of Ridgway's Hawk were observed constructing a nest at a site which was a short hike in to a mogote off the main road between Sabana Grande de Boya and Villa Riva (Dod 1978) The nest was a pile of twigs on a branch next to a bromeliad, 15m above the ground in the tallest tree in the area Both the male and the female brought in a twig The male dropped his off to the female at nest and watched her arrange it This was followed by a copulation on a nearby tree A female and a male collected by C B Cory at Almercen on August 24 and 27, 1883 are stored at the National Museum of Natural

History, Washington DC (USNM) and the Field Museum of Natural History, Chicago (FMNH) Elevation ranges from 14-134m asl

33-Sánchez / La Cañita, DR (19°14'08 46"N 69°36'52 47"W) This was an historical Ridgway's Hawk locality as cited in Dod (1978) and Wiley & Wiley (1981) Two specimens (a male and an unknown) collected at La Cañita by W L Abbott on July 14 and 15, 1883 are stored at the ANSP A male collected by Cory on December 15, 1905 is stored at The Natural History Museum (NHM), Tring, Herts, UK An immature female collected by W L Abbott on February 7, 1919 is stored at the USNM Elevation ranges from 29-327m asl

34-Las Terrenas, DR (*c* 19°18'31 11"N 69°32'38 03"W) This was an historical Ridgway's Hawk locality as cited in Wiley & Wiley (1981) Elevation ranges from 10-55m asl

35-Samaná, DR (19°13'03 88"N 69°20'24 32"W) This was an historical Ridgway's Hawk locality as cited in Dod (1978) An adult female and male were collected by Cory on April 3 and September 21, respectively (Cory 1883) and are stored at the NHM A specimen collected by W L Abbott on May 30, 1883 from "Samana Bay" is stored at the Academy of Natural Sciences (ANSP) Two males and two females, including the Type specimen, collected by Cory on April 3, 4, 10 and September 4, 1883 are stored at the FMNH Elevation ranges from 0-364m asl

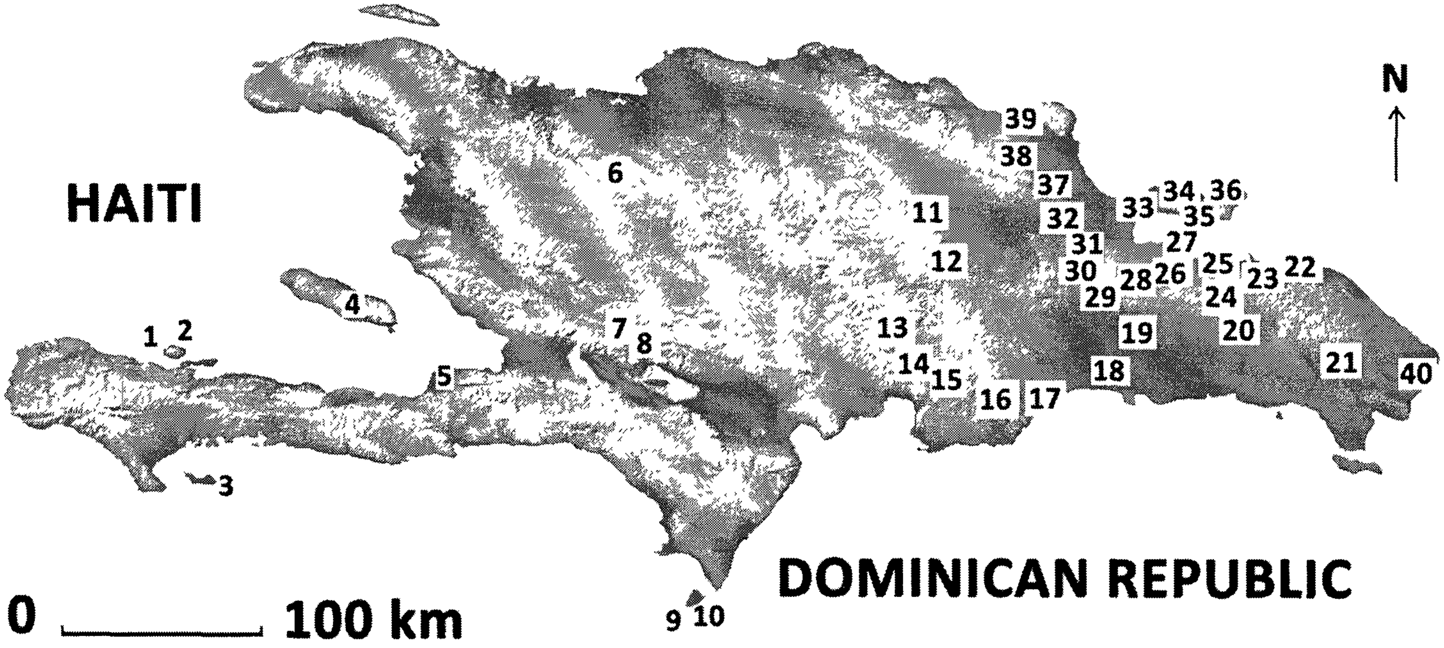
36- Samaná Peninsula, DR (19°14'10 46"N 69°19'48 83"W) A Ridgway's Hawk was heard calling by Miguel-Angel Landestoy, Pablo Weaver and Arlen Marmolejo on July 12, 2003 The locality was several kms north of Samana city, in the hills and along the river en route to the beach at El Valle Pablo Weaver's notes "The first "sighting" was on July 12, 2003 above the town of Samana We were collecting fish at the Rio San Juan, near Cascada Zumbador (19°14'11 30"N 69°19'48 55"W, 45m asl) It was morning, around 10 00am Miguel Angel Landestoy, who has a great ear for birds, heard the call of a Ridgway's Hawk Subsequently, Arlen Marmolejo and myself also heard the call, but we were shielded from a direct observation by the overhanging vegetation We were in a riparian area, surrounded by some farmland and open fields As I recall, the surrounding habitat was a mixture of large trees and open farmland, and was definitely a disturbed area The second sighting occurred the same day, July 12, 2003 at around 12 00 noon, near the Salto de Limon (19°15'47 24"N 69°27'14 69"W, 200m asl) We had hiked down to some of the waterfalls and were heading back to the trail head when we heard a Ridgway's Hawk call The bird soared overhead, and came to a perch in a large Coconut Palm tree As I recall, we were approximately 1 km from the trailhead, in a typical clear farmland environment, with some large trees scattered throughout, and some thicker riparian vegetation along the stream Miguel Angel Landestoy, Arlen Marmolejo and I all watched the Hawk, and Miguel was able to video tape the bird as it soared and perched in the Coconut Back at the trail head, we talked with some of the locals who definitely knew of the Ridgway's Hawk, and even imitated the call to us They said that the Hawk was very dangerous to their animals and themselves, because of its large claws"

37-Reserva Cientifica Loma Guaconejo, DR (19°19'22 48"N 69°58'1 50"W) There is a significant area (*c* 337km^2) of protected remaining karst rainforest between the Reserva Cientifica Loma Guaconejo and Loma Quita Espuela (19°22'10 67"N 70°08'51 89"W) This forest is between two historical sites (Villa Riva 8km to the south and Laguna Flaca 13km to the north) Although no confirmed records exist for Ridgway's Hawk at Quita Espuela or Guaconejo, this could be a potential site for future releases Elevation ranges from 43-750m asl

38-Laguna Flaca, DR (19°29'34 49"N 70° 6'28 78"W) This was an historical Ridgway's Hawk locality as cited in Wiley & Wiley (1981) Two males were collected at Laguna Flaca, SE Cabrera by J L Peters on August 3, 1916, and are stored at the Museum of Comparative Zoology, Harvard University, Cambridge, US Cabrera is a village on the coast *c* 15km to the northeast Elevation ranges from 52-237m asl

39-Los Cacaos, DR (19°35'16 12"N 70°05'04 38"W) This was an historical Ridgway's Hawk locality as cited in Wiley & Wiley (1981) Dod (1978) mentions an area called El Cacao but I have no idea if this is the same place Elevation ranges from 24-82m asl

40-Punta Cana, DR (18°33'42 53"N 68°20'42 43"W) Three juvenile hawks were translocated from Los Haitises to a private reserve at Punta Cana by The Peregrine Fund and Sociedad Ornitologica Hispaniola in 2009 There are no historical records from Punta Cana but there are records from Higuey, 37km to the west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Chapter 4

NESTING SITES AND BREEDING ECOLOGY

4.1 INTRODUCTION

Although Neotropical raptors are more taxonomically diverse than their North American counterparts (67 and 14 genera respectively; Bildstein et al. 1998), there have been relatively fewer ecological studies carried out in the Neotropics (Wiley & Wiley 1981, Mader 1982, Delannoy & Cruz 1988, Seavy & Gerhardt 1998, Thorstrom & Quixchan 2000, Thorstrom et al. 2001, Delannoy & Tossas 2002). In particular, studies on the nesting and reproductive biology of West Indian raptors have been limited (Wiley 1986) despite there being 48 species in this region.

Breeding ecology characteristics within *Buteo* are varied; ranging from medium-sized, monogamous migrants with high annual productivity (Swainson's Hawk *B. swainsoni* and Red-shouldered Hawk *B. lineatus*), to larger-sized, sedentary, co-operative polyandrous species with low annual productivity (Galapagos Hawk *B. galapagoensis*). In general, tropical raptors exhibit longer breeding episodes and lower reproductive rates than similar species in temperate regions (Newton 1979, Mader 1982, Delannoy & Cruz 1988). However, *Buteo* species do not always exhibit this pattern (White-throated Hawk *B. albigula*: Trejo et al. 2004).

Ridgway's Hawk is the rarest species in the genus *Buteo* (BirdLife International 2010) and is also one of the least known of raptor species. Once widespread and endemic to the island of Hispaniola, *B. ridgwayi* is now limited to a small area on the northeast coast of the island (see Chapter 3). *B. ridgwayi* has been historically recorded from a variety of habitats, from karst limestone primary forest to agricultural plantation (Wiley & Wiley 1981). Breeding episode observations have been very few. Three nesting attempts were documented by Wiley & Wiley (1981) but no comprehensive nest observations have been reported since then.

Addressing the lack of ecological knowledge for this declining species is critical to determine if ecological factors are contributing to the species decline. Identification of limiting factors linked to the ecology of the species (e.g. nesting or feeding requirements affected by habitat loss) can then be applied to the development of conservation management planning. This chapter analyses five years of research on nest sites and breeding biology of Ridgway's Hawk. Aspects of *B. ridgwayi* breeding ecology are discussed in relation to it's phylogenetically closest species, the Red-shouldered Hawk *B. lineatus* (Amaral et al. 2006, 2009) and the geographically closest forest *Buteo* species, the Puerto Rican Broad-winged Hawk *B. platypterus brunnescens*. Conservation management suggestions resulting from this research are presented in Chapter 9.

4.2 METHODS

4.2.1 Nest monitoring

Breeding pairs of *B. ridgwayi* were studied within Los Haitises National Park over five breeding seasons from January to July of 2005-2009 on the northeast coast of Hispaniola

(Chapter 2) Nest observations and breeding pair monitoring methodology are detailed in Chapter 2

A nest was defined as active once an egg had been laid An alternate nest was a nest that had been wholly or partially constructed, but with no egg(s) laid A nest was classified as successful if at least one young fledged and failed if it had been active but subsequently did not produce at least one fledgling Indications of nest failure were the absence of an attending adult during 2-4 hour observations on successive visits, or the death or disappearance of all eggs or nestlings Causes of nest failures were determined by a combination of nest observations, adult bird behaviour, and examination of the nest site, nest, and nest contents Nest contents were identified by viewing through a spotting scope or climbing to nests

Lay, hatch and fledging dates were based on nest observations and nest checks Females sat tight once the first egg had been laid and incubation period was therefore calculated from laying of the first egg to hatching of the last egg Nest attendance was defined as the total amount of time at least one adult was present at the nest Brooding was defined as the amount of time an adult was covering 50% or more of the nestlings Productivity was defined as the number of fledglings produced per active nest, while nest success was the proportion of nest attempts that fledged at least one young

Nestlings, juveniles and adults were banded whenever possible during all breeding seasons However, it was not possible to band all individuals Adults were trapped using a bal-chatri noose trap (Chapter 2) Nestlings were banded on the nests when between 25 and 35 days old. Hawks were banded with coloured aluminium identification bands. Different sized bands were required for males and females (Chapter 2).

4.2.1.1 Nest and site parameters

For each individual nest the following information was collected: Name of valley; GPS coordinates (WGS84); nest tree species; nest tree height using an optical range finder; nest tree circumference at breast height (CBH); nest height from bottom of nest to the ground using a measuring tape if the nest was climbed to, or an optical range finder; and nest orientation using a compass. We also recorded whether it was a first or second nest attempt for that pair in that year. Distances to nearest conspecific nest, and potential competitor's nests (White-necked Crow *Corvus leucognaphalus* and Red-tailed Hawk *Buteo jamaicensis*) were estimated using GPS coordinates and Google Earth ©. We also recorded whether the *B. ridgwayi* nest was constructed on top of a Palmchat *Dulus dominicus* nest (Figure 4.1), and if so whether the Palmchat nest was active or not.

Macrohabitat for each nesting site valley was divided into three categories: New *conuco*, Old *conuco*, and Secondary Forest (Fig. 4.1). New *conucos* were valleys that had recently been cleared and burned within the last 2 years for agriculture (primarily beans, maize and root crops such as manioc) and were being actively farmed at the time of the nest attempt. Old *conucos* were areas that had been cut in the past 3-10 years, but subsequently abandoned and were beginning to regenerate. They contained a mix of native plants such as *Cecropia* and agricultural species (Mango *Mangifera indica*, Banana *Musa* spp., Cacao *Theobroma cacoa*). Secondary Forest sites were areas that had been cut in the past 10-20 years but had been abandoned and allowed to regenerate. They contained a larger proportion of native tree species such as Higuillo *Piper* *aduncum*, Matchwood *Didymopanax morototoni,* Dominican mahogany *Swietenia mahagoni*, Silk cotton tree *Ceiba pentandra,* Masa *Tetragastris balsamifera,* American muskwood *Cuarea trichiloides*, Corcho bobo *Pisonia albida*, and Granadillo *Buchenavia capitata* There were no areas of primary forest left on the western side of the National Park where this study was carried out Small patches of primary forest still exist in the center and east of the park in areas that are relatively inaccessible

Indices for predator abundance and human activity were calculated for each nest by carrying out three 3-hour watches at each nest site The absolute number of potential predators, including active nests of other species observed within the nesting valley, and of people passing through the nesting territory were recorded during each watch A Territory Disturbance Index (TDI) was also calculated each year for each nesting territory This index estimated the level of direct human persecution to a pair within their territory, by compiling information collected during nest watches and from local landowners This index was divided into 3 categories Category 1 was used if there were no known direct disturbances to the breeding pair Category 2 referred to minimal to intermediate disturbance This could include people digging for root crops near the nest tree, or an isolated incident of boys throwing rocks at the nest or birds for amusement Category 3 included major disturbances to the pair, people using slingshots or throwing rocks at nests with intent to harm an adult or nestlings, knocking down nests, collecting nestlings for food, or direct attempts by landowners to kill hawks

Nests were measured when accessed to band nestlings, or once the nest had failed or young had fledged Nest measurements taken were exterior nest length, width and depth and outer and inner nest cup length, width, and depth Nest materials and contents were also described Length, width and mass of infertile and/or abandoned eggs were measured to the nearest 0 01 mm with Vernier Calipers and a 100g Pesola© spring scale to the nearest 0 1 g

4.2.2 Data analysis

Parametric tests were carried out whenever possible for their increased sensitivity and statistical power and distribution of residuals were tested for normality using Q-Q plots

4.2.2.1 Nest site parameters

Nest site parameters for active and alternate nests, and nest tree species were compared in univariate tests Continuous variables that met assumptions of normality were compared using t-tests Variables that violated the assumptions were $\log_e$ transformed prior to analysis or were analyzed using Mann-Whitney *U*-tests Pearson Chi-Square tests were used for categorical parameters Due to low sample size of alternate nests it was not possible to enter variables within a multivariate model

4.2.2.2 Nest attendance, success and productivity

The total number of minutes that an adult spent attending or brooding a nest was tallied and reported as the percent of total time observed A linear regression was used to test whether nest attendance or brooding durations were correlated to age of nestling(s)

To determine predictors of nest success, nest site parameters of successful and failed nests were initially compared with univariate tests Continuous variables that met assumptions of normality were compared using t-tests Variables that violated the assumptions were $\log_e$ transformed prior to analysis or were analyzed using Mann-

Whitney *U*-tests. Pearson Chi-Square tests were used for categorical parameters. All parameters that had a univariate P-value <0.25 were then entered into a multivariate model. For multivariate comparison of successful and failed nests, a logistic regression analysis was used to determine which combination of nest site parameters was most useful in predicting nest success.

A full factorial mixed-model ANOVA was used to analyze productivity among years and areas, with year as the fixed effect and area as the random effect. GLM ANOVA was used to compare productivity among nesting territories, with year included in the model for control.

For determining predictors of productivity, nest site parameters were initially compared in univariate tests. Continuous and categorical variables that met assumptions of normality were compared using GLM ANOVA tests. All parameters that had a univariate P-value <0.25 were then entered into a multivariate model. A full factorial GLM analysis was used to determine which combination of nest site parameters (along with their interactions) was most useful in predicting productivity.

A linear regression was used to test whether productivity of nesting territory was correlated to laying date. Mean productivity was calculated for each nesting territory over the study period and a linear regression was used to test whether mean productivity of a territory was related to the number of years it was active. Because any single year's nest may fail due to random events (e.g. weather, isolated predation or disturbance), 3+ years of data minimized the influence of such events and provided a more accurate representation of territory quality.

Values reported in the text are means ± SD unless otherwise noted. P values < 0.05 indicate a significant result, P values > 0.05 and < 0.10 indicate a trend. Data were analysed using SPSS statistical package (SPSS 2003).

4.3 RESULTS

4.3.1 Nest construction

Observations at nest sites began in January-February, at which time most pairs had already occupied nesting territories and were exhibiting signs of courtship. Courtship behaviours and copulations were observed during early nest construction (See Chapter 7 for mating behaviours).

Construction of nests was observed from 8 January through July 17. Nest construction was already underway by several pairs in early January when field research began, and therefore the earliest nest building dates are not known. However, with the nest construction stage ranging from 15 to 44 days (see below, this paragraph), and the earliest egg being laid January 15, it can be estimated that nest construction may have commenced in some pairs as early as the beginning of December. The latest date noted for construction of a first nest attempt was April 24. During the earlier stages of nest building, most pairs worked on more than one nest simultaneously (See Section 4.3.1.1). The length of time from beginning to end of construction on an individual nest varied among pairs, but generally took 2-3 weeks. Nest construction was observed in 39 pairs. Detailed observations for first nest attempts were recorded for 10 pairs. Duration of nest construction varied from 15 to 44 days and averaged 21.9 ± 11.8 days. It generally took 4-5 days for the pair to line the inner cup and complete the nest. Duration of nest construction for second nest attempts could not be estimated as often a second nest attempt was made using a nest that had already been partially constructed earlier in the season.

Both sexes participated in nest building. Nest material was most often collected from within 100m of the nest, within the same valley, although birds were on occasion observed flying out of sight toward an adjacent valley to collect material. Birds were observed breaking off twigs and large leaves using their bills, and carrying material in talons. Males tended to do the majority of building during the initial stages prior to shaping of the nest cup (71% of 56 observations). They generally brought in nest material and left it on top of the nest. The female became more involved during later stages, collecting materials, and more often arranging material at the nest. During the final 1-6 days of construction the female remained at the nest while the male delivered material. The female used her bill to arrange material in the nest, and then trampled the base of the nest with rapid foot movements to shape and line the inner cup with plant material (green and dried leaves, bromeliads, moss and lichen).

Depending on tree species, nests were supported by the bases of 3-7 palm fronds or by 3-6 large branches, 4-12cm in diameter. In order of abundance, nesting materials consisted of twigs, thin plant stalks and vines, bromeliad and orchid rootlets, dried bromeliad and banana leaves, moss, live greenery, and down feathers (Table 4.1; Figure 4.3.). The female lined the nest with down feathers just prior to laying and during early incubation.

4.3.1.1 Alternate nest construction

Pairs were observed constructing more than one nest simultaneously, generally within the same or adjacent valley. Data on alternate nests were collected opportunistically. Over half the pairs were observed exhibiting this behaviour to varying degrees, but not all nests could be followed in detail. Twelve alternate nests were found in 2006 (n=7 pairs) and 18 were found in 2007 (n=12 pairs). For the 19 pairs observed, number of alternate nests per pair ranged from 1-3. One pair was observed constructing three alternate nests simultaneously, before laying in a 4th nest. On three occasions, two nests were constructed simultaneously by juvenile pairs but no eggs were laid in either nest.

4.3.2 Nest sites

Fifteen nest site parameters (ten continuous and five categorical) were recorded for 246 *B. ridgwayi* nests constructed over a 5-year period: 216 active nests and 30 alternate nests (Tables 4.2 and 4.3). Active nest heights averaged 12.8 ± 4.6 m above the ground, in trees averaging 142.1 ± 40.0 cm in circumference (Table 4.2). Nest length and width averaged 93.4 ± 39.2 cm by 73.5 ± 28.4 cm respectively, with an average depth of 46.0 ± 16.4cm (Table 4.2). For active nests, distance between nearest breeding neighbour ranged from 199 to 1197 meters, and averaged 607 ± 267 meters (Table 4.2). For alternate nests, the distance to closest active nest ranged from 45 to 341 meters, with an average distance of 190 ± 71 meters (Table 4.2).

Ridgway's Hawks used 20 tree species for active nest sites: 78.4% were in *Roystonea hispaniolana* (Figure 4.1), 5.0% in *Spondias mombin*, 4.3% in *Sideroxylon foetidissimum*, 2.7% in *Ficus maxima*, 2.1% in *Clusia rosea* and < 0.5% in each of the remaining 15 other tree species (Table 4.3). The majority of active nests were facing north, with fewest facing southeast (Table 4.3). The macrohabitat type within the valley of 161 active nesting sites consisted primarily of Old *conuco*, followed by New *conuco* and Secondary Forest (Table 4.3). Ninety-one of 216 hawk nests (42%) were built on top of Palmchat nests. Sixty-four percent of the Palmchat nests with Ridgway's nests built on top were active (Table 4.3).

The nest cup was measured for 105 nests. Both the inner and outer dimensions of the cup were recorded. Outer cup measurements averaged 32.4 ± 7.0 cm by 25.4 ± 5.7 cm and 7.3 ± 1.4 cm deep. Inner cups measured 17.2 ± 2.4 cm by 14.2 ± 2.5 cm and 2.5 ± 1.0 cm deep (Table 4.5).

4.3.2.1 Active vs. Alternate nests and Royal Palm vs. Other nest trees

Nest tree CBH of active nests tended to be smaller than for alternative nests (p=0.056), (Table 4.2, Table 4.4). None of the other continuous variables differed between active and alternate nests. For categorical parameters, proportion of nest tree species used (Royal Palm vs. Other) and nest orientation did not differ between active and alternate nests (Table 4.3, Table 4.4).

There was a significant difference in nest tree height, nest tree CBH, and nest height between the favoured Royal Palm trees and other tree species (Table 4.4), with all three parameters being significantly less in Royal Palms.. Nest length showed a trend (p=0.08; Table 4.4), with nests constructed in Royal Palms being slightly longer (Table 4.4).

4.3.3 Nest defense and interspecific interactions by *B. ridgwayi*

B. ridgwayi aggressively defended their nests from avian intruders. The female was generally the more aggressive of the two, although both sexes were observed diving at intruders. Ridgway's Hawks were observed attacking Turkey Vultures *Cathartes aura* (19 observations), Red-tailed Hawks *Buteo jamaicensis* (two observations), Ashy-faced Owl *Tyto glaucops* (one observation), and Cattle Egret *Bubulcus ibis* (one observation). More detailed nest defense and interspecific interactions observed are detailed in Appendix 4.1.

4.3.4 Laying and incubation

Over the study period, laying of first clutches began January 15 and continued through April 14, spanning 89 days. The earliest lay date recorded was 15 January in 2008. There were only 5 nests that had laying dates in January over the 5-year study period, with the majority of breeding pairs laying in February. Average lay date was Feb 20 ± 15.3 days (n=44). The latest date recorded for laying of a first clutch was 14 April in 2006.

Date of laying first clutches did not vary significantly among years ($F_{4,41} = 0.593$, p= 0.62). There were too few degrees of freedom to determine if there were any differences in lay dates among pairs within the seven areas of the park monitored during the 5-year period.

Clutch sized ranged from 1 to 3 eggs (Table 4.6). Average clutch size laid over the five year period was 2.0 ± 0.4 (n=84). The most common clutch size was 2 (n=63), followed by clutches of 1 (n=12). There were 9 clutches with 3 eggs. The majority of eggs were laid 2 days apart (e g 16th and 18th, n=31), with eggs also being laid 3 (n=8) and 4 (n=2) days apart Eggs were short oval in shape (see Harrison 1975), and were cream coloured with light brown to rusty-brown speckles, blotches and streaks concentrated at the larger end There was quite a range in the extent of these markings among eggs, with some eggs much less heavily marked than others (Figure 4 3)

Egg dimensions were recorded for 21 eggs (n=16 nests) and were 48 02 ± 2 16 mm (44 25-51 86 mm) by 39 11 ± 0 98mm (38 21-41 35 mm) Average egg weight was 33 46 ± 4 63 grams (n=20) and ranged from 24 8-39 1g, 8 2% of female body mass (see Chapter 7, average female body mass was 402g, n=21), and 24 6% of her mass for a clutch of 3

Length of incubation ranged from 33 to 37 days with an average length of 34 9 ± 1 1 days (n=34) Females performed the majority of the incubation, however the males were also found to incubate for significant amounts of time The time spent incubating by males varied from 5 to 250 minutes

4.3.5 Nest attendance, hatching and nestling development

Hatching was asynchronous and ranged from 1-3 days apart For the majority of clutches, eggs hatched two days apart (e g 16th and 18th, n=48) with eggs also hatching 1 (n=8) and 3 days apart (n=3) Over the 5-year period, brood size varied from 1 to 3 and averaged 1 4 ± 0 7 (Table 4 6) The most common brood size was 2 (n=109), followed by broods of 1 (n=41) There were five broods with 3 nestlings

Hatching of eggs in real time was observed at four nests that were easily visible In two of these, the female was observed eating the pieces of hatched eggshell during and immediately after hatching In both cases the total amount of shell consumed could not be determined, but did not appear to be all of the pieces

Upon hatching, nestlings were dark grey, wet, and very weak Within two hours the female would generally have preened the new hatchling so that it was covered in dry greyish-white down Eyes were partially open within 3 hours of hatch After 3-6 hours, hatchlings were able to lift their heads up, open gapes, and beg The female generally gave the first feeding to the new hatchling within 4-6 hours of hatch

Initially nestlings were quiet at the nest, and spent most of the time prostrate Once the young were 2-3 days old they were more active within the nest, and attending females preened the young several times an hour By this time nestlings could be heard producing quiet high-pitched squeaks during begging At this point the attending female began leaving the nestlings for short periods of < 10 minutes every 2-3 hours, either standing on the edge of the nest or flying to perch on a favoured observation tree 10-20m from the nest, from which she could watch the nestlings like the proverbial hawk By 6-8 days old, young were able to move clumsily around in the nest, and could back up to the edge of the nest to defecate over the rim They also began self-preening at this age By days 11-13, nestlings could stand up on their own to stretch, flap wings or peck at items in the nest Pin feathers were becoming visible in place of the grey down, beginning at the primary wingtips (Figure 4 4) Females continued to brood nestlings until they were 15-20 days old, at which time they were becoming too large for the female to physically brood At this point, most of the female's time at the nest was spent feeding the nestlings By days 17-23 nestlings were approximately 1/2 the size of the attending female, primaries were 1/4 to 1/3 out of feather sheaths, rectrices were emerging, and some body feathers had emerged on the back. By days 29-32, chicks were typically nearly full-sized and fully feathered, excepting the head and parts of the chest, with flight feathers nearly or fully grown. By the time the chicks were 38-40 days old they were in full juvenile plumage, and very independent. The female would still return to the nest to help feed the young. Length of the nestling period ranged from 41- 50 days with an average length of 47.1 ± 2.2 days (n=42).

In 14 nests where only 1 of 2 eggs hatched, the egg was left in the nest. In some cases it may have been pushed to the nest's edge, but was not removed during the entire nestling stage.

Adult nest attendance at the nest was negatively correlated to nestling age ($R^2 = 0.63$, $p<0.00$). However, females were rarely seen to travel further than 50m from the nest, during the entire nestling stage, unless the male was in attendance at the nest. Similarly, the amount of time adults spent brooding decreased significantly as nestlings aged ($R^2 = 0.79$, $p<0.00$). Males were not observed brooding, but they did attend the nest with nestling(s) for short periods of time ranging from 2 to 21 minutes.

During banding, nestlings were frequently observed to be parasitized by botfly *Philornis pici*. Of 132 nestlings that were either banded on the nest or observed soon after death, 43% (57/132) were parasitized by *P. pici*. An additional thirteen percent of nestlings had scars from earlier infestations, but were not parasitized at the time of handling, for a total of 56% of nestlings having had some degree of parasitism. The average number of botfly on a parasitized nestling was 13.3 ± 10.2 (n=57). Forty percent of parasitized nestlings (23/57) were covered with 20 or more larvae. Twelve nestlings died over the 5-year period from excessive botfly infestation around the bill, throat and chest. However, neither the presence of botfly nor the quantity of botfly was found to be an overall predictor of the subsequent fledging success of an afflicted nestling (presence of botfly: $\chi^2_1 = 0.27$, $p = 0.59$; quantity of botfly: $F_{1,56} = 1.14$, $p = 0.37$). Eleven nestlings that were heavily infested (20-45 botfly) went on to fledge successfully.

4.3.6 Fledging

Over the study period, 36 nests fledged 1 chick, 49 nests fledged 2 chicks, and 1 nest fledged 3 chicks. Fledging of nestlings began as early as mid-April and continued through July. For 4-12 days prior to first flight, young perched on the nest edge and hopped or flapped to nearby palm fronds or branches. In some cases, young had moved 1-3m from the nest, on fronds or branches of the nest tree, prior to taking their first flights. Nestlings took their first flights from the nest tree when 41-50 days old. Mean age at fledging was 47.1 ± 2.2 days (n=42). Initial first flights were an awkward glide to nearest tree 10-15m from the nest, although some first flights did involve flapping and no loss in altitude. On occasion, fledglings would end up on or near the ground during their first flight and had to hop back up to higher branches of the canopy.

4.3.7 Breeding episode

The breeding episode for Ridgway's hawk from initiation of nest construction to fledging of the young can now be estimated at 110-130 days. During the 5-year period, no pair was observed to fledge more than one successful brood per year. Two stages in the hawk's breeding cycle still remain somewhat unclear: the length of time from the initiation of courtship behaviours to nest construction, and the length of time from fledging until dispersal of young from the natal territory. Observations by the local research team during the non-breeding season suggest that pairs likely occupy a territory year round. However more detailed observations need to be carried out from August-December, to confirm the extent of territoriality during the non-breeding season.

4.3.8 Nest success and productivity

4.3.8.1 Nest success

A total of 216 active nesting attempts were monitored from 2005 to 2009 (Table 4.6). Of these, 133 nests produced 221 nestlings and 86 nests produced 137 fledglings. Reproductive success was 61.5% for the incubation period, and 64.7 % for the nestling period. Nest success varied annually from 37.5 % to 45.8 % over the 5 years, averaging 40.5 % (Table 4.6). There was no significant variation in nest success from year to year or among areas (year: $\chi^2_4 = 0.55$, p= 0.97, area: $\chi^2_6 = 6.62$, p= 0.36). There was a significant difference in nest success among individual nesting territories ($\chi^2_{60} = 60.06$, p= 0.00).

4.3.8.2 Temporal and spatial variation in productivity

Over the study period, total productivity (number of fledglings/active nest) was 0.64 ± 0.10 (Table 4.6). Productivity was not correlated to laying date (Adjusted $R^2 = -0.029$, p=0.18; Figure 4.5) and did not vary significantly among years or areas (year: $F_{4,211}=0.12$, p=0.97, area: $F_{6,211}=1.31$, p=0.28, area*year: $F_{24,211}=0.98$, p=0.49). However, there was a significant difference in productivity among individual nesting territories ($F_{60,203}=2.06$, p=0.01) indicating that certain territories consistently produced more young than others. Productivity was not correlated with number of years a nesting territory was active (Adjusted $R^2 = -0.004$, p=0.94; Figure 4.6) and this was also confirmed by field observations that birds returned to monitored nesting valleys, and individual nest trees, regardless of nest success the previous year. One pair used the same nest after three successive years of nest failures in the same nest. The ten most productive nesting territories (representing 25% of the breeding population) produced 40% of the fledglings. The ten least productive nesting territories produced 2% of the fledglings. In general, there was relatively high adult mortality and high turnover rate for pairs (Chapter 3), therefore this measure is most likely representative of territory quality and not pair quality

4.3.8.3 Predictors of nest success and productivity

Only one continuous and one categorical variable exhibited univariate P-values < 0.25 for comparing successful with failed nests (Table 4.7). The final logistic regression model, controlling for year and area, found territory disturbance to be a significant predictor of nest success, with nest height as a potential predictor (disturbance: $\chi^2_2 = 5.57$, $p= 0.018$, nest height $\chi^2_1=3.41$, $p=0.09$). There was significantly less disturbance to successful nests. Nests which were higher in nest trees showed a trend of being more successful than nests lower in trees (Successful nest average height: 14.03 ± 3.67m, n=66; Failed nest average height: 12.10 ± 4.01m, n=107).

Similarly, one continuous and one categorical variable showed univariate P-values < 0.25 when comparing productivity of nests (Table 4.8). The final GLM ANCOVA model found territory disturbance to be a significant predictor of nest success, and nest height as a potential predictor (Table 4.9). The nests with the least amount of disturbance produced significantly more young. Nests higher in trees showed a trend toward producing more young.

To explore the potential trend between nest height and nest success and productivity, data were plotted (Fig.4.7). The plot indicated a pattern of variation at two height levels: nests ≤10m and nests >16m. Further analysis found significant differences in nest success and productivity for nests ≤10m compared to nests >10m (nest success: χ^2_1 =5.61, p=0.01, productivity: $F_{1,172}$ = 6.58 p=0.01). Significant differences were also found in nest success and productivity for nests >16m compared to nests ≤16m (nest success: χ^2_1=6.72 p=0.01, productivity: $F_{1,172}$ = 9.09, p<0.00). Of 44 nests with heights ≤10m: 78% failed, 13% fledged one young, and 9% fledged two young. By comparison, of 15 nests with heights >16m: 11% failed, 24% fledged one young, and 65% fledged two young.

Predator abundance and human activity were not predictors of nest success or productivity (Table 4.8). Neither number of potential avian predators observed, nor number of people passing through the nesting territory affected the nest outcome. Similarly, macrohabitat type, presence or status of a Palmchat nest, and distance to nearest conspecific nest were not predictors of nest success or productivity.

4.3.9 Nest failures and renesting

4.3.9.1 Nest failures

Of the 216 nests monitored during the 5-year study period, 130 failed to fledge young. Stage of nest failure was identified for 83 of these 130 nests. Twenty-one nests failed during incubation. Fifty-one nests failed during the nestling stage. A further 11 nests could not be accessed but were known to have failed during either late incubation or early nestling stages (Table 4.10). For the remaining 47 nests, the stage at which nest failure occurred was not determined and these were classified as unknown.

The cause of nest failure was identified for 51 out 130 nests (Table 4.11). Confirmed and suspected incidences of human disturbance accounted for 43.1% and 17.6% of all known nest failures, respectively. Confirmed human disturbances included; nest trees burned or cut down (3 cases), nests intentionally knocked down (4), confirmed cases of poaching or killing of eggs/nestlings (5), and abandonment due to excessive human activity such as rocks and sticks thrown at the nest (6), or cutting and burning near the base of the nest tree (2). Suspected human disturbances included the disappearance from nests of older healthy nestlings during successive years at sites where landowners were openly known to persecute the hawks (6), or where people were suspected of poaching nestlings for food (2). Local people were generally vocal when they did not like the hawks, and it was well known within the village of Los Limones which landowners persecuted the hawks. Rumors also generally circulated within the village soon after nestlings were poached for food. It was accepted practice that nestlings were left in the nest until near fledging, in order to be as large as possible when harvested for food.

Other confirmed causes of nest failures, in order of occurrence, included: six incidents of all nestlings dying from Botfly *Philornis pici* infestation, infertile eggs (5 nests), death of young nestlings from exposure during heavy rains and winds (4 nests), and nests falling to the ground due to a broken supporting palm frond (4 nests).

Other causes of nest failure suspected by the author but not confirmed were: predation by Red-tailed Hawk *Buteo jamaicensis jamaicensis*, Stygian Owls *Asio stygius noctipetens*, Ashy-faced Owl *Tyto glaucops* and Hispaniolan Boa *Epicrates striatus,* unidentified disease, and disturbance by nocturnal animals (owls, boas, *Rattus rattus*) causing brooding females to flush from the nest at night and unable to return leading to death of young nestlings from exposure. In five cases, eggs or apparently healthy young nestlings (< 2 weeks old) were observed in an afternoon check, and the next morning the female was not incubating or brooding and nestlings had disappeared (3 cases) or were found dead in the nest (2 cases). There were an additional four nests where apparently healthy older chicks (5-6 weeks old) were found dead in the nest, cause unknown, and three cases where they disappeared from the nest completely, suggesting either disease, predation by Red-tailed Hawks, or poaching for food as potential causes.

4.3.9.2 Renesting

Renesting after nest failures occurred from mid-February through July. The proportion of monitored pairs that renested after their first nest failed ranged from 26% (9/35) in 2008 to 45% (19/42) in 2007, and averaged 35.4% over the study period. Ridgway's Hawks renested after failures during both incubation and nestling stages. Although not common, four pairs were observed renesting even after nests had failed with older feathered nestlings. There were no recorded observations of 3rd nesting attempts.

Thirteen of 58 second nesting attempts (22.4%) went on to be successful. Of the 45 failed nests, 11 (24.4%) failed at the egg stage and 23 (51.1 %) failed at the nestling stage. Stage of failure was not determined for the remaining 9 nests (20.0 %). Nesting trees used for second nest attempts were between 20.0 and 562.0m from the first attempt (= 222.3 ± 157.8m, n = 32).

During the peak of the breeding season (February-June), the shortest interval between a nest failure and second nesting attempt was nine days. The first nest attempt failed during incubation. The second nest attempt was laid in an alternate nest that had already been partially constructed earlier in the season. The time span between a nest failure and laying of a replacement clutch ranged from 9 to 39 days.

4.3.10 Post-fledging dependency and age at first breeding

For the first few days after fledging, the young returned to the nest after small flights. Parents continued to bring food back to the nest. Two female fledglings from a nest in 2007 continued to return to the nest and eat food provided by the adults several weeks post-fledging. Both fledglings were seen in the natal valley 23 days post-fledging, calling constantly. When the adult male returned to the nest with food, both fledglings followed him to grab the food. The fledglings were also observed hunting on their own by this time. One of these same young birds was observed in the natal valley 44, 52, 62 and 72 days post fledging, perched 390-550m from the nest. However, these observations from a single nest attempt should not be considered a definitive length of time for post-fledging dependency for this species, and is an aspect of the species' biology that requires further research.

Earliest recorded age for first breeding was one year for males and two years for females. A female banded as a nestling in 2005 laid two eggs in 2007. Her nest attempt was 2.47 km from her natal nest. She paired with a young male that had been banded as a nestling in 2006, on a nest 2.66km from their nest attempt. One egg hatched and the nest failed with an old nestling. The male was killed by local people, and the young female was unable to feed the nestling on her own.

A male and a female, both banded as nestlings in 2005, constructed two nests in 2007 but did not lay. In 2008, they produced two fledglings in a nest in the same 2007 territory.

Their successful nest in 2008 was 30 and 80m from their 2007 nests. The successful nest was 625m from the male's natal nest, and 1090m from the female's natal nest.

A male banded as a nestling in 2007 paired in 2009. His nest attempt failed with two nestlings. This nest was 1.72km from his natal nest. A male banded as a nestling in 2006 paired in 2009. His first and second nest attempts failed with two and one nestlings, respectively. These nests were 38m from each other, and 1.29km and 1.33km from his natal nest.

4.4 DISCUSSION

4.4.1 Nesting sites

4.4.1.1 Nesting trees

Nesting trees of *B. ridgwayi* were predominantly Royal Palm trees or emergent native hardwoods. Neotropical raptors have been most commonly reported to nest in emergent native hardwoods (*B. platypterus*: Delannoy & Tossas 2002; Hengstenberg & Vilella 2005, *Accipiter bicolor*: Thorstrom & Quixchan 2000; *B. jamaicensis* in Puerto Rico: Santana et al. 1986). There are no other published accounts of neotropical raptors using palm trees for the majority of their nesting sites.

There are few historical records of *B. ridgwayi* nest attempts or descriptions of nesting trees. Wetmore & Lincoln (1934) described a partially built nest 10m above the ground in a Royal Palm. Bond (1928) mentions two nests with downy young in Haiti in April as 7.6m and 12.2m high, but no mention is given of nest tree species. Wiley & Wiley (1981) described three nests: two in standing dead hardwood trees partially enclosed by *Clusia rosea*, and one nest in a live *Buchenavia capitata*. One of these three nests was on top of a Palmchat nest. Dod (1992) observed construction in February of a partially constructed nest 40 feet above the ground. The nest was in a clump of bromeliads in a strangler fig. Dod describes a second nest in April with two "white fluffy" nestlings "high in a tall tree", which would presumably be a hardwood. This second nest was on top of an active Palmchat nest.

Palm trees in the Genus *Roystonea* are native to most islands of the West Indies, with 90% of the 250+ plus species being West Indian island endemics (Zona et al. 2007). The morphology of *Roystonea hispaniolana* may provide a clue as to why this palm is used so often by Ridgway's hawk as nesting trees. The base of the palm fronds is wide, much more so than any of the other palm species in Hispaniola. The fronds are also strong, again more so than any of the other palm species in Hispaniola. This combination provides a stable, large area for nest construction. The fronds also provide physical shelter from rain and from the sun, again making them favorable nesting trees. Finally, in coastal karst rainforest, the Royal Palm is abundant, particularly in the study area on the western side of Los Haitises, where other large emergent endemics have been cut down. However, even on the eastern side of the forest which is less degraded, Royal Palms were being used by *B. ridgwayi* as nest trees (author pers. obs.).

Forty two percent (91/216) of active Ridgway's Hawk nests found in this study were constructed on top of Palmchat nests. These large (up to 1.5m wide) colonial nest structures provided a large platform support for the nesting hawks. The relationship between the two species appears to be somewhat beneficial to both species. The hawks are reptile specialists and rarely catch Palmchats as food (~2% of the hawks prey items, see Chapter 5, Table 5.3). The hawks aggressively defend the site, deterring other potential Palmchat predators from the area The Palmchats appear to be tolerant of nesting hawks and were regularly seen to continue adding material to their colonial nests, and did not abandon, even after hawks had started building their own nests Palmchat nests were most often constructed in Royal palms but were also found in emergent hardwood trees Ridgway's hawks were found nesting on top of Palmchat nests both in Royal Palms and in emergent hardwoods

B platypterus inhabits forests in Puerto Rico with similar structure to Los Haitises, including a mix of emergent hardwoods and a very similar species of palm tree, the Puerto Rican Royal Palm *Roystonea borinquena*, yet there are no published records of Broad-winged Hawks nesting in palm trees Although there are no bird species in Puerto Rico that build large colonial nests similar to those of the Palmchat, *B playpterus* will commonly nest on the large platform-type structures created by termite nests Five of 11 (45 5%) *B platypterus* nests described in Puerto Rico in 2005 were on top of termite nests (Hengstenberg & Vilella 2005) This percentage is similar to the proportion (42%) of *B ridgwayi* nests built on top of Palmchat nests during the current study

Nesting tree availability for Broad-winged Hawks in Puerto Rico was high, with an average of 85 suitable trees per 4ha (Delannoy & Tossas 2002) This is clearly not the case for Ridgway's Hawk where each nesting valley (2-5ha) contained at most *c* 15-25 potentially suitable nesting trees (author pers obs) In addition to the already low number of potential trees in undisturbed areas, annual cutting and burning of the forest further has reduced the number of potential nest trees in each valley

4.4.1.2 Nests

Ridgway's Hawk nests measured in the current study were larger than the two nests described by Wiley & Wiley (1981), and larger than those of other similar sized raptor species in the neotropics (Thorstrom & Quixchan 2000, Hengstenberg & Vilella 2005). This is likely due to the use of Palmchat nests and palm trees which provide larger support areas on which nests can be built, relative to the forks or horizontal branches of hardwoods most commonly used by other neotropical raptors for nest construction (Delannoy & Tossas 2002, Hengstenberg & Vilella 2005, Thorstrom & Quixchan 2000, Santana et al. 1986).

During the current study, Ridgway's Hawks were observed lining their nests with fresh greenery throughout the egg and nestling stages. This was also recorded by Wiley & Wiley (1981) and has also been noted in *B. lineatus* (Dykstra et al 2009a), *B. platypterus* (Hengstenberg & Vilella 2005) and the insular Hawaiian Hawk *B. solitarius* (Griffin et al. 1998). There have been several hypotheses proposed in the literature as to why raptors continue to furnish their nests with greenery during the breeding cycle. During incubation, fresh plant material may act as a buffer between eggs and the nest substrate, although this is not likely to be necessary for *B. ridgway*i as the nest cup is generally already thick and soft, being well furnished with dried plant material prior to laying. During nestling stages, fresh plant material may help raise nestlings above the level of fecal sacs, provide camouflage, reduce odor, and decrease parasite loads (Wimberger 1984). The author suspects that the latter hypothesis may be the most likely possibility and recommends further research of any correlation between amount of fresh greenery brought to the nest and parasite loads, particularly for tropical fowl mite *Ornithonyssus bursa* which was recorded on nestlings in the current study. Clark (1991, cited in Dykstra et al. 2009a) found that removal of greenery from European Starling *Sturnus vulgaris* nests resulted in an increase in mite abundance. Similarly, Shutler & Campbell (2007) found that experimentally adding greenery to Tree Swallow *Tachycineta bicolor* nest boxes reduced flea infestation. *B. lineatus* line their nests with Black Cherry *Prunus serotina* leaves which emit hydrogen cyanide and other insecticidal chemicals when damaged (Dykstra et al. 2009a).

This is the first documentation of *B. ridgwayi* building several nests simultaneously within their nesting territories. This behaviour of 'alternate' nest construction has been reported in other temperate and neotropical raptor species (*Buteo* spp.: Griffin et al. 1998, Sergio 2002, Dykstra et al. 2009b; *Accipiter* spp.: Reynolds et al. 2005, Thorstrom & Quixchan 2000; other Falconiformes: Seavy et al. 1998, Steeger & Ydenberg 1993). *B. buteo* nesting pairs have been recorded constructing as many as 7 alternate nests in a territory (Sergio 2002), while *B. lineatus* normally constructs 2-3 (Dykstra et al. 2008). Alternate nests within a territory are usually accumulated over several seasons, and can be used over consecutive years (Sergio 2002, Dykstra et al. 2008). The fact that both temperate and tropical *Buteos* exhibit this behaviour can rule out the hypothesis that alternate nest construction has evolved due to more extreme weather in the tropics. This study found one instance of *B. ridgwayi* laying in an alternate nest just nine days after the loss of their first clutch.

4.4.2 Breeding episode

The timing of the breeding episode for Ridgway's Hawk coincides with most breeding pairs having nestlings over 3 weeks old in May-June as the wet season begins. This timing may help ensure the prey base is abundant enough to provide for older nestlings. This timing is somewhat earlier than reported for Broad-winged Hawks *B. platypterus* in

Puerto Rico, and Bicolored Hawks *Accipiter bicolor* in Guatemala, with incubation recorded most often during the dry season, and fledging generally coinciding with the beginning of the wet season (Hengstenberg & Vilella 2005, Thorstrom & Quixchan 2000). Mader (1982) notes that some raptor species will occasionally nest during both wet and dry seasons, and recorded Bicolored Hawks constructing nests in May, at the start of the rainy season and fledging young during the peak of the wet season. This was also observed for *B. ridgwayi* during the current study, with several nests fledging young in August of each year, several months after the start of the wet season.

Although the total length of the breeding cycle for *B. ridgwayi*, from commencement of courtship behaviours to dispersal of young from the natal territory was not determined, the time from construction of nests to fledging spanned 110-130 days. The Red-shouldered Hawk subspecies *B. lineatus elegans* in California has a breeding episode that spans over 150 days excluding post-fledging dependency (Wiley 1975), but including the establishing of nesting territories prior to nest construction. The breeding cycle for *B. platypterus* in Puerto Rico was reported as approximately 188 days (February to July), from nest construction to dispersal of young (Hengstenberg & Vilella 2005). This is comparable to the Puerto Rican Sharp-shinned Hawk *Accipiter striatus venator* breeding cycle of 184 days (Delannoy & Cruz 1988). The entire breeding cycle of Ridgway's Hawk is likely similar, if the post-fledging period is confirmed to be approximately two months, as anecdotal observations suggest.

Longer breeding episodes have been documented in raptors of comparable size and feeding requirements in tropical latitudes, than in their temperate counterparts (Mader 1981; Santana & Temple 1988; Delannoy & Cruz 1988). The longer breeding period of the neotropical Bicolored Hawk (188 days) compared to the temperate Cooper's Hawk (132 days) was due to an earlier nest building and courtship stage by Bicolored Hawks in February, with egg laying not occurring until April (Mader 1981, Thorstrom & Quixchan 2000). Similarly, Sharp-shinned (Delannoy & Cruz 1988) and Broad-winged Hawks (Hengstenberg & Vilella 2005) in Puerto Rico have an extended period between nest site occupancy and laying that accounts for a longer breeding cycle than their temperate subspecies. Anecdotal evidence suggests that Ridgway's Hawks also have this extended period, with pairs observed in territories in November-December, but not laying until February (Hilario Jorge Pollanca & Timoteo Bueno Hernandez pers comm).

4.4.2.1 Incubation stage

Length of the incubation period for *B. ridgwayi* can now be documented at *c*.35 days (ranging from 33-37), which is consistent with other neotropical raptors (del Hoyo et al. 1994). Although females are the primary incubator, males also spend a considerable amount of time incubating, depending on the pair. It was common for some males to incubate continuously for more than three hours. Similar behaviour was noted in the White-throated Hawk *B. albigula* and Broad-winged Hawk *B. platypterus* (Trejo et al. 2004, Henstengberg & Vilella 2005) with males incubating up to 2.5 hours and more than four hours, respectively. This behaviour is not well documented in the neotropics as the males of most neotropical raptors are rarely observed incubating (Newton 1979, Thorstrom & Quixchan 2000, Schulze et al. 2000). In the temperate *B. lineatus*, Ridgway's Hawk closest relative, the female carries out the majority of the incubation (Dykstra et al. 2008). One potential hypothesis for the behaviour of male incubation in Ridgway's may be the high density of prey items in the nesting territory which allows female Ridgway's to hunt and capture prey relatively quickly on their own. Short forays from the nest may have evolved in to longer periods away from the nest, while males incubate. There was considerable difference in the amount of time a male incubated among individual pairs, similar to that seen in prey provisioning (see Chapter 5). For some pairs, the male routinely incubated for up to 3 hours, while in others only the female was observed incubating. It appeared that the female was responsible for determining how long a male incubated (pers obs). In this situation, it may also be that an older, more experienced female may prefer to hunt on her own, if her male is younger and less able to provide regular feedings. This hypothesis could be tested in the future, as more and more birds within the study group are banded.

Neotropical raptors generally produce smaller clutches than those in temperate areas (Lack 1947, 1948; Newton 1979). The mean clutch size of 2.0 ± 0.4 for *B. ridgwayi* in the current study is slightly larger than for the three nests described by Wiley & Wiley (1981) and also somewhat greater than clutch sizes of other similar sized raptors in the tropics (Delannoy & Tossas 2002, Panasci & Whitacre 2002). This is due to the occurrence of three-egg clutches in *B. ridgwayi*, first documented by Thorstrom et al. (2007). Nine of 84 (10.7%) nests with known clutch sizes during the current study contained three eggs. Both the neotropical Roadside Hawk *B. magnirostris* and Puerto Rican Broad-winged Hawk produce 1-2-egg clutches (Panasci & Whitacre 2002, Delannoy & Tossas 2002). The closely related temperate Red-shouldered Hawk *B. lineatus* lays clutches of 1-5, with the more southern subspecies' of *B. lineatus* laying smaller clutches of 1-3 (Dykstra et al. 2008; Wiley 1975). Avian clutch sizes are thought to be limited by food availability and/or predation pressures (Lack 1947, 1948; Skutch 1967). Experimental brood manipulations of Savanna Hawks *Buteogallus meridonalis* found that food limitation was likely the main factor limiting clutch size (Mader 1982).

For Ridgway's Hawk, natural nest predation (non-human) was observed to be low during the study, and food availability high (see Chapter 5). This would have likely been similar throughout the hawk's historical range in the coastal karst rainforest of Hispaniola. Relatively lower predation pressures on Hispaniola, and an adequate food supply may have potentially selected for 3-egg clutches in *B. ridgwayi*.

4.4.2.2 Nestling stage and fledging

Length of the nestling period for Ridgway's Hawk can now be documented at *c.*47 days (ranging from 41-50), which is slightly longer than that reported for most other similar sized neotropical raptors (del Hoyo et al. 1994). Young of Broad-winged Hawks *B. platypterus* in Puerto Rico fledge at 37-45 days (Hengstenberg & Vilella 2005) and *Accipiter bicolor* fledge at 30-36 days old. Temperate *B. lineatus* fledge between 30-45 days old depending on geographic location, with more southern subspecies having longer nestling periods (Dykstra et al. 2008).

During the current study, one pair fledged three young. Two other cases of three fledglings were recorded in 2002 (Thorstrom et al. 2007). Four other three nestling broods were recorded during the current study, but all failed prior to fledging. In all cases, starvation was not the cause of failure: three nests were suspected to be poached by people with healthy nestlings near fledging; one nest failed with older nestlings, possibly due to disease, with large amounts of uneaten prey items in the nest. This suggests that *B. ridgwayi* could be capable of fledging three young with current food availability, and this is supported by food provisioning data collected over the 5-year period (Chapter 5).

4.4.2.3 Post-fledging period

The duration of post-fledging to dispersal from the natal territory for *B. ridgwayi* is still unknown, as is the fate of birds once they disperse from the area. There is virtually no unoccupied habitat for young birds to disperse too.

There is little in the literature regarding post-fledging dependency in neotropical raptors. Thorstrom & Quixchan (2000) radio-tracked four fledgling Bicolored Hawks, following them for 4-9 weeks until they dispersed out of range. Mader (1982) found post-fledging periods of ten months in the White-tailed Hawk *B. albicaudatus* and seven months in the Great Black Hawk *Buteogallus urubitinga*.

Temperate *Buteo* species appear to have shorter post-fledging periods (Newton 1979). Woofinden and Murphy (1983) found young Ferruginous Hawks *B. regalis* to disperse from their natal territories 20-30 days after fledging. Mader (1981) suggests that the onset of migration contributes to a shortened period of fledgling dependence in temperate *Buteos*. This is supported by Snyder and Wiley (1976) who found longer post-fledging dependency periods in resident *B. lineatus* in California (10 weeks), compared to their more northern migratory counterparts (6 weeks). A long dependency period in the tropics may provide added parental care and increased chances of survival for smaller, less frequent broods, which would seem to be the case for Ridgway's Hawk.

4.4.3 Nest success and productivity

The nest success of 40% found in this study was higher than the 34% reported by Thorstrom et al. (2007) for Ridgway's Hawk from 2002-2005. The similar sized Broad-winged Hawk and Sharp-shinned Hawk of Puerto Rico were found to have 50% and 29% nest success, respectively. Puerto Rican Sharp-shinned Hawks suffered not only from high nestling mortality, but also desertion of clutches (Delannoy & Cruz 1988), which was not seen to be a factor in *B. ridgwayi* nest failures.

Productivity of *B. ridgwayi* during this study (0.64 fledglings/nest) was nearly identical to that reported by Wiley & Wiley in 1981 (0.66) and Thorstrom et al. in 2007 (0.60). Productivity for *B. ridgwayi* was similar to the two *Buteo* subspecies on Puerto Rico; Broad-winged Hawk with 0.66 fledglings /nest (Delannoy & Tossas 2000) and Red-tailed Hawk with 0.70 fledglings/nest (Santana & Temple 1988). However, the productivity of *B. ridgwayi* is nearly three times lower than that of its most closely related species *B. lineatus*. This is not unexpected as *B. lineatus* is a temperate, migratory species.

Productivity varied among Ridgway's Hawk nesting territories. Productivity in raptors has been attributed to prey availability (Newton 1979) and predator abundance (Sergio et al. 2003). An index of prey densities was collected during this study by measuring rates and biomass of prey delivered to nestlings (see Chapter 5). The results indicated that there were no food shortages within the study area during the 5-year period, and no association between prey delivery rates and either nest success or productivity (see Chapter 5, section 5.3.2).

There was also no correlation between the predator abundance index measured during the study period and *B. ridgwayi* productivity. Presence of avian predators can reduce productivity of smaller raptors, as has been recorded for Black Kites *Milvus migrans* fledging no young when nesting <1 km from Eurasian Eagle Owl *Bubo bubo* nests (Sergio et al. 2003). Although Ridgway's Hawks aggressively defended their nest territory from aerial species, the final outcome of the nest was not related to avian predator abundance. Broad-winged Hawks in Puerto Rico also aggressively and successfully deterred intruding Red-tailed Hawks from their nesting territories (Hengstenberg & Vilella 2005). Red-tailed Hawks are capable of killing adult Ridgway's Hawks and are suspected during the present study to have been nest predators. Red-tailed Hawks depredate adults of other raptor species including owls and falcons (Bahm & Sullivan 2009). Prey of the Red-tailed Hawk overlapped only slightly with that of Ridgway's Hawk, consisting mostly of rats (Wiley & Wiley 1981), and larger birds such as Plain Pigeon *Columba inornata*, which Ridgway's Hawks were not observed to hunt. Lizards, the main prey of Ridgway's Hawk (Chapter 5) were infrequently found in Red-tailed Hawk nests (Wiley & Wiley 1981). Although White-necked Crows have also been considered a potential nest predator of the hawk (Wiley & Wiley 1981), there were no observations of hawks attacking crows, and the author does not believe that crows were capable of forcing Ridgway's hawks from their nests.

As was the case for Broad-winged (Delannoy 1997) and Red-tailed Hawks (Santana et al. 1986) in Puerto Rico, most Ridgway's Hawks nests were in close proximity to human activity. There was an extensive trail system throughout Los Haitises National Park, similar to the Rio Abajo Forest of Puerto Rico (Delannoy & Tossas 2002). Most valleys within Los Haitises were used to some extent for root crop cultivation. There is a traditional land use system within the Park with most valleys being "owned" by local villagers. To determine to what extent *B. ridgwayi* were able to tolerate different levels of human activity, Human Activity and Territory Disturbance Indices were collected for each nest attempt. Nest success and productivity were not affected by normal human activity (i.e. people walking through a territory, working near nest). *B. ridgwayi* were able to tolerate fairly extensive human activity within their territory and to successfully fledge young while utilizing small (<2ha) fragments of forest within human altered habitat, as long as they were not directly persecuted. Hawks in areas where they were persecuted showed outward signs of disturbance (standing, alarm calling, flushing, flattening in nest, or looking around in agitation) when people were nearby. These behaviours were not observed in territories where hawks were not persecuted. Wiley (1986) noted that *B. ridgwayi* had been historically recorded in varying degrees of human altered habitat types. Thorstrom et al. (2007) also recorded pairs occupying pasturelands, coconut plantations, and forest edge habitats. This adaptability to human altered habitats, as long as some forest habitat remains to provide nesting sites and food, has likely been a contributing factor to their continued survival in the Dominican Republic (see Chapter 9). Ridgway's Hawk is closely related to Red-shouldered *Buteo lineatus*, and Broad-winged Hawks *B. platypterus*, (Amaral et al. 2009); both of which are woodland *Buteo* species adaptable to a range of human-altered habitats (del Hoyo et al. 1994, Dykstra et al. 2000, 2001). Fortunately, Ridgway's Hawks have persisted within the final sanctuary of Los Haitises, despite increased human activity and habitat modifications.

4.4.4 Nest failures

Known causes were confirmed for 40% (51/130) of nest failures. Weather, including heavy rains and winds, was the cause of four known nest failures (7.8%). Periods of heavy rainfall caused nest failures of Sharp-shinned Hawk in Puerto Rico (Snyder & Wiley 1976, Delannoy & Cruz 1988). Nest failure from hurricanes and heavy rains did not pose a serious threat for *B. ridgwayi* during the study period. A species with a relatively long reproductive lifespan, relatively high natural productivity, and early age of first breeding would not normally be affected by stochastic events, such as cyclones. However, if the effective population size continues to decline to a handful of breeding individuals with only one source area, *B. ridgwayi* may become increasingly at risk to stochastic events such as severe and unpredictable weather.

Nest failure due to infertility or dead embryos was low at 9.8%. The actual number of infertile eggs may be higher as ten nests failed during the incubation stage of unknown causes, and nests were not accessed in time to discover why. Even so, infertility was low in nests that failed during the incubation stage that could be accessed. This is encouraging as small populations can be seriously compromised by conditions associated with bottlenecks and inbreeding, including low fertility (Frankham 1998; Swinnerton 2001) or embryo mortality (Glenn et al. 1999). The small remaining population of Takahe *Porphyrio hochstetteri*, exhibits hatch success rates of only 30%, due to inbreeding depression (Jameison et al. 2003) while infertility rates in the Pink Pigeon *Columba mayeri* are greater than 50% (Swinnerton 2001). Genetic evidence suggests that *B. ridgwayi* has recently experienced a bottleneck (Chapter 6) and that inbreeding is occurring in the population (Chapters 6 & 7). However, this reduction in effective population size does not appear to have resulted in low fertility or high embryo mortality.

Botfly *Philornis pici* parasitism accounted for 11.7% of *B. ridgwayi* known nest failures during the present study, with 56% of observed nestlings having been parasitized. The Puerto Rican Sharp-shinned Hawk also exhibited similar parasitism rates with 55% of nestlings parasitized between 1979 and 1985 (Delannoy & Cruz 1991). Annual nest failure rates in the Sharp-shinned Hawk averaged 66% but were variable (13%-100% depending on the year).

Impacts of parasites on vertebrate populations are predicted to be particularly severe in the tropics (Connell 1971 cited in Moller 1998). The nestling parasite *Protocalliphora* spp. has been recorded from Ridgway's closest relative *B. lineatus* (Sargent 1938), but is not mentioned as causing nestling mortality (Dykstra et al. 2008). *Philornis* spp. have a predominantly Neotropical distribution and parasitize nestlings of a range of avian species from passerines (Rabuffetti & Reboreda 2007) to raptors (Delannoy & Cruz 1991). In the Galapagos, the introduced *Philornis downsi* parasitized the majority of nests of endemic endangered finches (Fessl & Tebbich 2002, Dudaniec et al. 2007). The nest failure rate from *P. downsi* infestation was 41% for Darwin's Medium Tree Finch *Camarhynchus pauper* (O'Connor et al. 2010).

During the present study, there was a notable difference among years in number of *B. ridgwayi* nest failures due to *Philornis*, with many more larvae found on nestlings, and more nestling deaths in 2009 than in previous years. Nestlings that died from botfly had large numbers of botfly (20 or more) concentrated near the bill, neck and chest. Other nestlings were able to survive large numbers of larvae if located on the wings, back, abdomen or head. *Philornis* species may increase in number under conditions of higher precipitation (Arendt 1985). Rainfall during the 2009 season was greater than in previous seasons (Timoteo Bueno Hernandez pers. comm.) but a more detailed study of climatic conditions and botfly parasitism is required in order to test this hypothesis.

Human persecution was the main cause of Ridgway's Hawk nest failures during the present study, with both confirmed and highly suspected cases accounting for 60.7% of known failures. Thorstrom et al. (2007) also concluded that most *B. ridgwayi* nest failures were due to human activity including; slash and burn agriculture, deliberate cutting of nesting trees, poaching nestlings for food, and direct persecution of hawks at nest sites. From 2003-2005, 13 adult hawks were killed because of the misconception that they prey on poultry. One villager claimed to have killed more than 100 hawks in a ten-year period. In California, *B. lineatus* suffered high rates of nest failure due to poaching of nestlings for falconry (Wiley 1975). In Puerto Rico, direct human persecution of raptors was not a significant limiting factor, although some illegal hunting did occur, and a few nests were destroyed during road clearance (Delannoy & Tossas 2002). Most nest failures in *B. platypterus* were due to either weather or predation (Hengstenberg & Vilella 2005). The misconception that Ridgway's Hawks are significant poultry predators has led to the unfortunate persecution of *B. ridgwayi*, and is the most likely reason for the species' rapid population decline throughout Hispaniola. This misconception is fuelled by confusion with the larger, sympatric Red-tailed Hawk, which does kill chickens. Many villagers thought that Ridgway's Hawks were young Red-tailed Hawks. Others believed that both Ridgway's Hawks and Red-tailed Hawks would prey on young children.

Seventy-eight percent of nests ≤10m above the ground failed. By comparison, 89% of nests ≥16m fledged one or more young successfully. The strong association between nest success and nest height could suggest that a large percentage of the 'Unknown' nest failures were also caused by direct human persecution, such as throwing rocks at nests.

The other potential causes of nest failure (predation, disease, weather, parasites) would not likely be so nest height specific.

The majority (39%) of *B. ridgwayi* nest failures occurred during the nestling stage. In the case of Ridgway's Hawk, natural nest predation rates are low and human persecution is the main cause of failures. Increased diurnal activity during the nestling stage does have the potential in this case to increase delectability of nests by local people.

4.4.4.1 Renesting

Ridgway's Hawks were found to renest after first nest attempts failed with eggs and nestlings. Renesting after the loss of eggs has been reported in several neotropical raptor species (Hengstenberg & Vilella 2005, Delannoy & Tossas 2000, Thorstrom & Quixchan 2000, Mader 1982) but no reports of renesting after the loss of young. Renesting of North American buteonines after the loss of eggs is common, yet only one North American hawk, Harris' Hawk *Parabuteo unicinctus,* is reported to renest after loss of young (Mader 1975). This species also ranges into the neotropics. There are no reports of temperate *B. lineatus* or the Puerto Rican subspecies of *B. platypterus* renesting after loss of nestlings.

The ability of Ridgway's Hawks to successfully renest after loss of nestlings may reflect the relatively stable environmental conditions, and high density of prey available in Hispaniola. Ridgway's Hawks are sedentary with pairs most likely remaining near their nesting territories year round. A combination of these factors presents an extended period available for breeding. Although not yet reflected in the literature, it is reasonable to extend this hypothesis to other neotropical raptors. It would not be unexpected that future research on neotropical raptors would provide further evidence of renesting after loss of nestlings.

4.4.5 Conclusions

Nest success and productivity of the remaining population of *B. ridgwayi* were comparable to, and in many cases greater than, those of other similar-sized neotropical raptors. Reproductive parameters do not appear to be a contributing factor to the species' decline. The lack of evidence for compromised productivity (infertility, dead embryos) is also encouraging. Natural nest failure from predation, parasites, and weather have not been a major limiting factor for the species, although caution is required to ensure that such factors do not become a problem if the population continues to decline to even lower levels. Human persecution and habitat loss from unsustainable resource use, although major challenges, can be addressed, and reflect a larger environmental need to protect the remaining lowland coastal karst rainforest of Los Haitises, not solely for the hawks but for the region's unique biodiversity.

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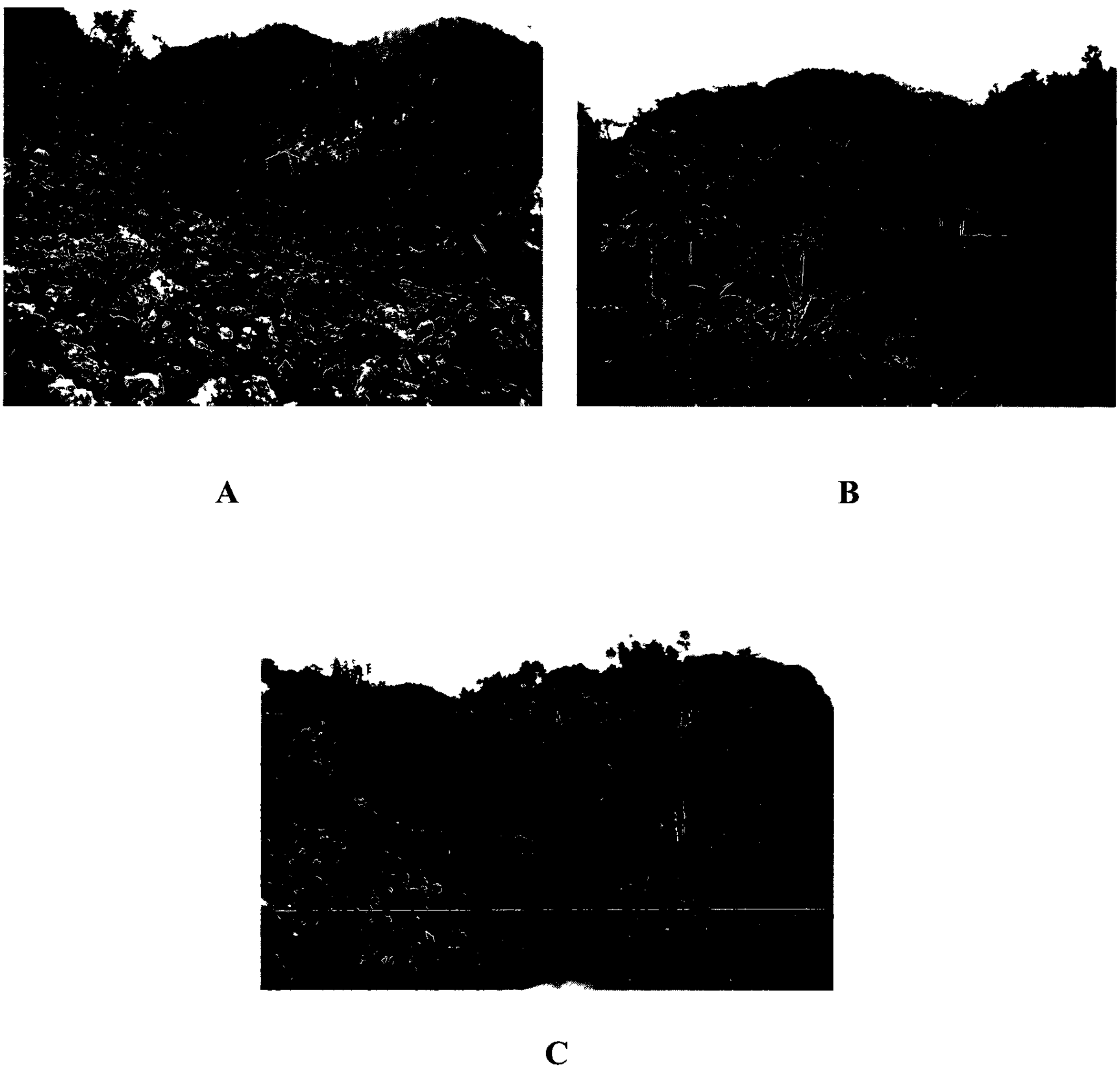


Figure 4.1 Macrohabitat types used by nesting Ridgway's Hawk in Los Haitises; (A) New *conuco*, (B) Old *conuco* and (C) Secondary Forest. Photos by Lance Woolaver.

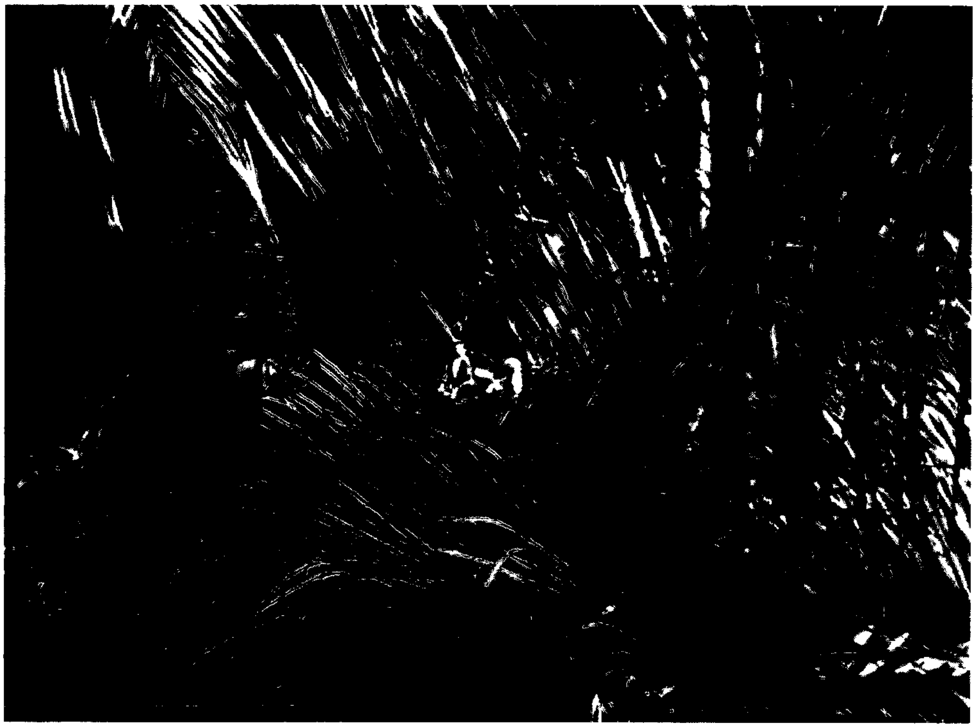
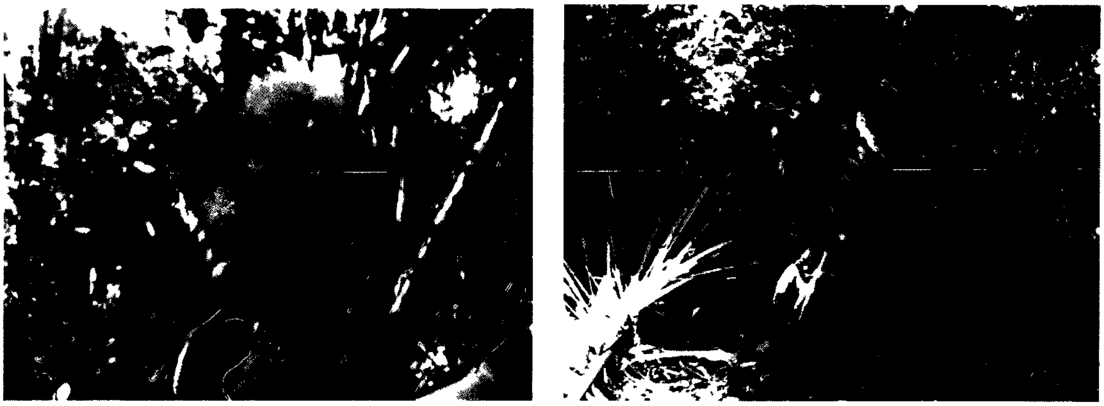


Figure 4.2 Photo of a Ridgway's Hawk nest (in red circle) on top of a Palmchat *Dulus dominicus* nest in a Royal Palm *Roystonea hispaniolensis*. Photo by Jorge Brocca.

Figure 4.3 Photo of a Ridgway's Hawk nest with three eggs. Photo by Lance Woolaver.

5 days old **16 days old**



25 days old **45 days old**

Figure 4.4 Photos of Ridgway's Hawk nestlings at different ages (5, 16, 25 and 45 days old). Photos by Timoteo Bueno Hernandez.

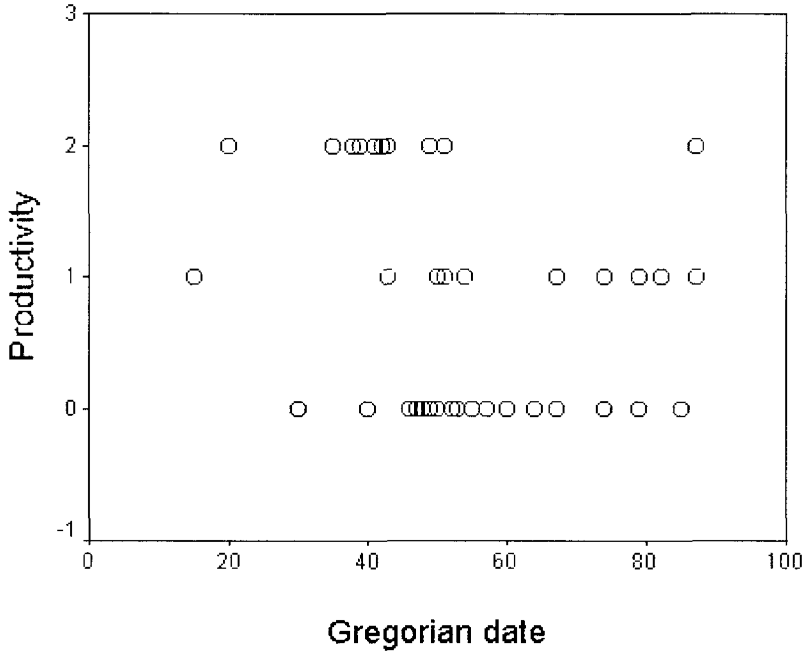


Figure 4.5 Productivity of *B. ridgwayi* nesting territories as a function of lay date. Adjusted $R^2 = -0.029$, $p=0.18$.

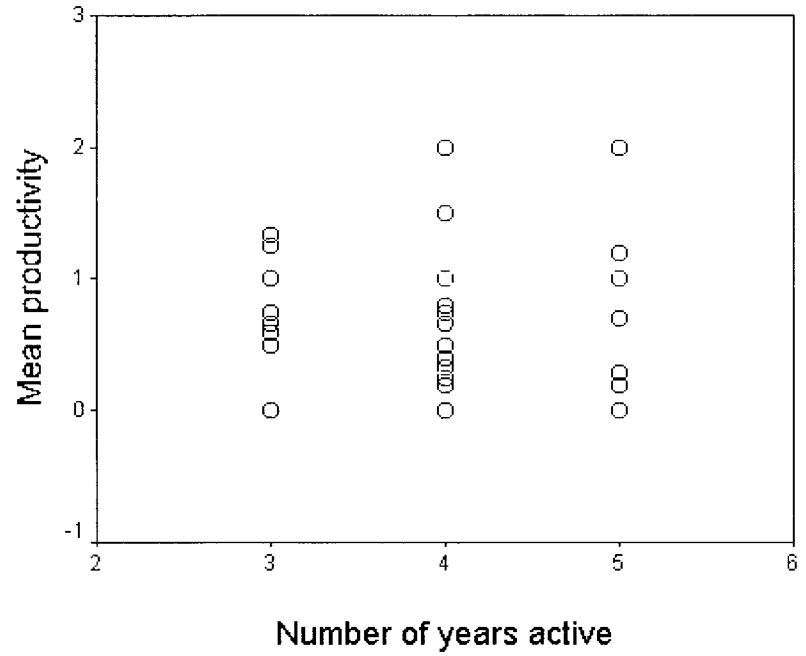


Figure 4.6 Mean productivity of *Buteo ridgwayi* nesting territories as a function of the number of years the territory was active. Only nest areas active in at least 3 of the 5 years of the study are included. Adjusted R^2 = -0.004, p=0.94.

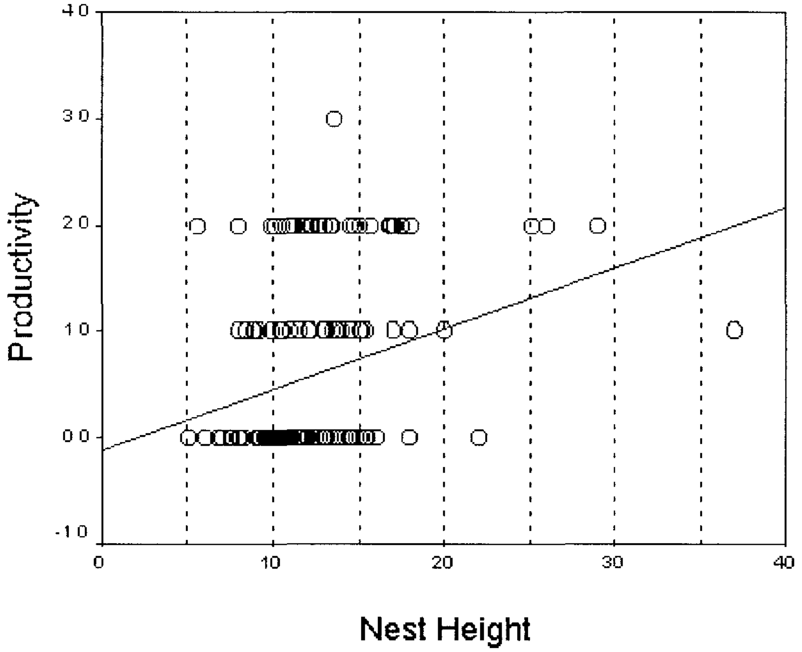


Figure 4.7 Productivity of Ridgway's Hawk nesting territories as a function of nest height (m). Adjusted $R^2 = 0.264$, $p=0.06$.

Table 4.1 Nesting materials of active nests from 2006-2008. Values refer to mean percent of nest volume.

Nesting materials	**Mean ±SD %**	**Range**	**n**
Twigs	60 ± 12	49-89	15
Thin stalks and vines	25 ± 9	19-33	15
Roots of Bromelids and Orchids	11 ± 5	6-15	15
Dried leaves (Bromelids, Banana)	10 ± 5	5-15	15
Live greenery	7 ± 3	0-10	15
Moss and Lichen	5 ± 2	0-8	15
Down feathers	2.5 ± 1	2-4	15

Table 4.2 Nest site parameters (continuous variables) for active and alternate Ridgway's Hawk nests monitored from 2005-2009. Field research in 2008-2009 was limited to active nests, thus the 30 alternate nests were recorded from 2005-2007. Human Activity and Predator Index variables were only collected for active nests.

Nest site parameter	Mean	SD	Range	n
Active nests (n=216)				
Elevation (m asl)	221.1	43.4	58.0 – 338.0	179
Nest tree height (m)	15.9	5.6	7.0 – 45.0	167
Nest tree circumference (cm)	142.1	40.0	50.0 - 350.0	172
Nest height (m)	12.8	4.6	5.0 –37.0	173
Nest length (cm)	95.4	32.9	50.0 – 185.0	108
Nest width (cm)	73.5	28.4	30.0 – 150.0	106
Nest depth (cm)	46.0	16.4	29.0 – 89.0	42
Distance to nearest breeding neighbour (m)	607	267	199 – 1197	140
Human Activity Index	4.3	2.3	0 – 15	123
Predator Abundance Index	3.5	2.4	0 – 21	117
Alternate nests (n=30)				
Elevation (m asl)	233.0	41.0	134.0 – 283.0	28
Nest tree height (m)	17.7	8.0	10.0 – 40.0	27
Nest tree circumference (cm)	205.1	80.5	85.0 – 500.0	26
Nest height (m)	14.3	7.4	8.0 –35.0	25
Nest length (cm)	99.6	23.4	75.0 – 165.0	11
Nest width (cm)	78.7	18.7	60.0 – 135.0	11
Nest depth (cm)	41.4	21.2	32.0 – 87.0	11
Distance to first active nest attempt (m)	190	71	45 – 341	19

Table 4.3 Categorical nest site parameters for active and alternate Ridgway's Hawk nests monitored from 2005-2009. Field research in 2008-2009 was limited to active nests. Macrohabitat type, Palmchat nest status and Territory Disturbance Index were only collected for active nests.

Nest Site Parameters	**Active Nest** **n (%)**	**Alternate** **n (%)**
Nesting tree species (Active, n=184; Alternate, n= 29)		
Royal Palm *Roystonea hispaniolana*	142 (78.4)	22 (75.8)
Jobo *Spondias mombin*	9 (5.0)	1 (3.4)
Hijo *Ficus maxima*	7 (4.3)	0 (0)
Calla *Sideroxylon foetidissimum*	5 (2.7)	2 (6.8)
Cupey *Clusia rosea*	4 (2.1)	0 (0)
Remaining 15 species[a]	17 (<0.5% each)	4 (4.5% each)
Nest Orientation (Active, n= 169; Alternate, n=28)		
North	55 (32.5)	10 (35.7)
Northeast	7 (4.1)	1 (3.4)
Northwest	18 (10.6)	4 (13.7)
East	17 (10.0)	2 (6.9)
West	18 (10.6)	4 (13.7)
South	38 (22.5)	6 (20.7)
Southeast	3 (1.7)	2 (6.9)
Southwest	7 (4.1)	1 (3.4)
Center	6 (3.6)	0
Macrohabitat type (n=161)		
Old *conuco*	77 (47.8)	-
New *conuco*	47 (29.2	
Secondary Forest	37 (23.0)	
Palmchat nest status (n= 91)		
Active	63 (64.9)	-
Inactive	28 (35.1)	
Territory Disturbance Index (n=148)		
1 = None	56 (37.9)	-
2 = Minimal to Intermediate	38 (25.7)	
3 = Major	54 (36.4)	

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[a] Chicharrón *Terminalia domingensis,* Coconut *Cocos nucifera,* Cigua blanca *Nectandra coriacea*, Amacey *Tetragastris balsamifera*, Cacao cimarrón *Sloanea berteriana*, Ceiba *Ceiba pentandra,* Grisgris *Bucida buceras*, Llalla prieto *Guatteria blainii*, Seibón *Bombacopsis emarginata,* Palo amargo *Margaritaria nobilis,* Llagrumo *Cecropia peltata*, Capa *Cordia alliodora*, Pancho prieto *Ziziphus rhodoxylon*, Guama *Inga vera*, and Palo maria *Calophyllum calaba.*

Table 4.4 Statistical tests of effect of nest site parameters on nest use (Active vs. Alternate) and nest tree species (Royal Palm vs. Other nest trees).

	Dependent Variable					
	Active Nest vs. Alternate Nest			**Royal Palm vs. Other nest trees**		
Elevation (m asl)	t = -1.19	df = 204	P = 0.24^a	t = 0.82	df = 169	P = 0.41^a
Nest tree height (m)	t = -1.43	df = 198	P = 0.16^a	**t = -7.90**	**df = 160**	**P = 0.00^a**
Nest tree CBH (cm)	**t = -1.98**	**df = 196**	**P = 0.056^a**	**t = -3.44**	**df = 165**	**P = 0.01^a**
Nest height (m)	t = -1.33	df = 198	P = 0.19^a	**t = -9.57**	**df = 191**	**P = 0.00^a**
Nest length (cm)	U = 321.0		P = 0.53^b	U = 160.5		P = 0.08^b
Nest Orientation	χ^2 = 7.62	df = 10	P = 0.67^c	χ^2 = 4.97	df = 9	P = 0.84^c
Tree Species	χ^2 = 0.38	df = 1	P = 0.54^c	--		

^{a} t-test

^{b} Mann Whitney U test

^{c} Chi-square test

Table 4.5 Nest cup measurements of active Ridgway's Hawk nests from 2005-2009.

Nest cup measurements	**Mean**	**SD**	**Range**	**n**
Outer cup length (cm)	32.4	7.0	20.0 - 60.0	102
Outer cup width (cm)	25.4	5.7	15.0 - 53.0	9
Outer cup depth (cm)	7.3	1.4	4.0 - 10.0	50
Inner cup length (cm)	17.2	2.4	12.0 - 22.0	61
Inner cup width (cm)	14.2	2.5	9.0 -22.0	54
Inner cup depth (cm)	2.5	1.0	1.0 - 5.0	52

Table 4.6 Annual reproductive rates of Ridgway's Hawk breeding pairs monitored from 2005-2009.

	Year					
	2005	**2006**	**2007**	**2008**	**2009**	**Total**
Active nests (No. of breeding pairs)	24 (19)	48 (34)	61 (42)	39 (28)	44 (35)	216
Mean clutch size (No. nests)	2.1 ± 0.5 (12)	1.9 ± 0.6 (13)	2.0 ± 0.5 (22)	1.9 ± 0.3 (23)	1.8 ± 0.3 (14)	2.0 ± 0.4 (84)
Mean brood size (No. nests)	1.5±0.9 (22)	1.5±0.6 (33)	1.3±0.9 (43)	1.3±0.8 (25)	1.6 ± 0.6 (33)	1.4±0.7 (156)
No. total fledged young (No. nests)	19 (11)	27 (18)	41 (23)	23 (16)	27 (18)	137 (86)
Productivity per active nest	0.79	0.56	0.67	0.59	0.61	0.64 ± 0.2
No. successful nests (%)	11 (45.8)	18 (37.5)	23 (37.8)	16 (41.0)	18 (40.9)	86 (40.6)

Table 4.7 Results of univariate tests for the effect of nest site parameter on the outcome of a Ridgway's Hawk nesting attempt (Successful or Failed). P values <0.25 are in bold.

Dependent variable (binomial) : Successful / Failed nest

Elevation (m asl)	t= 0.30	df= 175	P= 0.76
Nest tree height (m)	t= 0.84	df= 163	P= 0.41
Nest tree CBH (cm)	t= -0.27	df= 169	P= 0.78
Nest height (m)	**t= 2.04**	**df= 171**	**P= 0.043**
Nest length (cm)	t= 0.25	df= 104	P= 0.80
Nest width (cm)	t= 0.24	df= 102	P= 0.81
Distance to nearest active conspecific nest (m)	t= 0.25	df= 136	P= 0.80
Human Activity Index	t= 0.72	df= 114	P= 0.47
Predator Index	t= 0.21	df= 121	P= 0.83
Territory Disturbance Index	**$\chi^2 = 24.2$**	**df= 1**	**P= 0.001**
Tree species	$\chi^2 = 1.02$	df= 1	P= 0.31
Nest orientation	$\chi^2 = 8.01$	df= 9	P= 0.52
Macrohabitat type	$\chi^2 = 1.16$	df= 2	P= 0.56
Palmchat nest presence	$\chi^2 = 0.03$	df= 1	P= 0.87
Palmchat nest status	$\chi^2 = 0.06$	df= 1	P= 0.80

Table 4.8 Results of univariate tests for the effect of nest site parameters on Ridgway's Hawk productivity. P values <0.25 are in bold.

Dependent Variable: Productivity				
Source	**Type III SS**	**df**	**F**	**P**
Elevation (m asl)	0.078	1, 177	0.11	0.74
Nest tree height (m)	0.533	1, 163	0.80	0.37
Nest tree CBH (cm)	0.084	1, 169	0.12	0.73
Nest height (m)	**2.913**	**1, 171**	**4.49**	**0.036**
Nest length (cm)	0.390	1, 104	0.51	0.48
Nest width (cm)	0.430	102	0.18	0.67
Distance to nearest breeding neighbour (m)	0.097	1, 137	0.13	0.72
Human Activity Index	10.66	1, 114	1.16	0.27
Predator Index	8.370	1, 123	0.91	0.54
Territory Disturbance Index	**15.82**	**2, 144**	**21.8**	**0.001**
Tree species	0.587	1, 182	0.83	0.37
Nest orientation	5.360	9, 189	0.82	0.60
Macrohabitat type	1.006	2, 160	0.68	0.51
Palmchat nest presence	0.044	1, 211	0.06	0.81
Palmchat nest status	0.704	1, 83	1.04	0.31

Table 4.9 The effect of nest height and territory disturbance, controlling for year and area, on Ridgway's Hawk productivity.

Dependent variable : Productivity

Source		**Type III SS**	**df**	**MS**	**F**	**P**
Intercept	Hypothesis	550	1	.550	.604	.450
	Error	12.99	4.26	.911		
Year	Hypothesis	1.185	4	.296	.456	.768
	Error	61.050	94	.649		
Area	Hypothesis	3.766	6	.538	.82	.566
	Error	61.050	94	.649		
Disturbance	Hypothesis	6.229	2	3.115	4.79	.010
	Error	61.050	94	.649		
Nest Height	Hypothesis	1.843	1	1.843	2.93	.085
	Error	61.050	94	.649		

Table 4.10 Stage of breeding cycle during which nest failures occurred in *Buteo ridgwayi*, 2005-2009. Data is presented as number of nests with % in parentheses.

	Year					
	2005	**2006**	**2007**	**2008**	**2009**	**Total**
Incubation	3	3	6	4	4	21 (16.2)
Nestling	7	11	10	12	11	51 (39.2)
Late incubation/ early nestling [a]	3	1	4	1	2	11 (8.5)
Unknown	0	15	18	6	8	47 (36.1)

[a] These were nests known to fail just before or after the expected hatch date.

Table 4.11 Causes of failures in *Buteo ridgwayi* nests monitored from 2005-2009. Data is presented as number of nests.

	Year					
	2005	**2006**	**2007**	**2008**	**2009**	**Total**
Failed nests	**13**	**30**	**38**	**23**	**26**	**130**
Active nests	**24**	**48**	**61**	**39**	**44**	**216**
Weather	0	2	0	1	1	4
Confirmed human disturbance	5	4	4	6	3	22
Suspected human disturbance	1	1	2	3	2	9
Infertile	0	0	2	2	1	5
Botfly	0	1	0	1	4	6
Nest fallen from tree	0	1	2	0	2	5
Unknown	7	21	28	10	13	79

APPENDIX 4.1 Observations of nest defense and interspecific interactions involving Ridgway's Hawk, 2005-2009.

The most frequent observations were of attacks on Turkey Vultures. Turkey Vultures were commonly observed passing within metres of active hawk nests. In some cases this was accidental, when a vulture circled in order to gain height. In other cases this was clearly intentional with vultures swooping within 1m of a nesting female, at very high speeds. One incident occurred in which several vultures made successive quick passes at a nesting female, over a 40 minute period. The female was brooding two 6 day-old nestlings, and was clearly distressed at the vulture activity. Whether the vultures were interested in the nestlings or in prey remains at the nest was unclear.

Both males and females routinely attacked Turkey Vultures that trespassed within hawk nesting territories. If a female was incubating or brooding young nestlings and unable to leave the nest, then the non-attending male was the attacker. If the nest contained older nestlings, both male and females attacked vultures, with the female generally being the more aggressive. Attacks were made from above with hawks swooping down on top of the vultures, swerving away just before any contact.

The only times that females showed signs of being distressed while on the nest, were when Turkey Vultures flew overhead, usually when circling within 40m or less while trying to gain altitude. In these cases, the female would lie flat in the nest, emit alarm calls, and look around and up rapidly in clear agitation. This behaviour was not observed in the presence of any other avian species. Turkey Vultures are a relatively recent coloniser of Hispaniola (Latta et al. 2006) and it is likely that this behaviour has evolved as a response to larger avian predators such as Red-tailed Hawks or potentially an extinct avian predator such as *Titanohierax* or *Amplibuteo*.

Red-tailed Hawk territories were located near the furthest edges of the study area and relatively little time was spent observing Ridgway's Hawk nests that were in close contact with Red-tailed Hawks. However adult Ridgway's Hawks were twice observed attacking Red-tailed Hawks and Red-tailed Hawks were suspected to have been nest predators during the present study.

In 2007, a pair of Ashy-faced Owls nested in a Royal palm that had been used as a nest tree in 2006 by Ridgway's Hawks. In 2007, the Ridgway's pair nested in another Royal Palm 143m from the active owl nest. An aggressive interaction was observed in April, when both nests contained older nestlings. After the adult owl left the nest and perched nearby, the adult male hawk dove at the owl. The owl flew to another perch, after which the hawk dove again and struck the owl with its talons. The owl nest fledged a single young while the hawk nest failed with two nestlings.

We observed three avian species attacking Ridgway's Hawk: American Kestrel *Falco sparverius dominicensis* (two occasions), White-necked Crows *Corvus leucognaphalus* (11 occasions), and Gray Kingbird *Tyrannus dominicensis* (two occasion).

White-necked Crows and Ridgway's Hawks commonly nested in the same valley, within 30-110m of each other. Nesting Ridgway's were not seen to exhibit distress behaviours in the presence of crows, even when crows passed within metres of an active hawk nest. Conversely, crows were observed harassing hawks. Crows were most often seen attacking Ridgway's Hawks in a group, with 2 or 3 crows attacking lone hawks.

In territories that were known to be persecuted by local people, Ridgway's Hawks flushed from nests and emitted alarm *Kleeah* calls when people passed nearby. Hawks were never observed attacking humans passing near the nest. Adult males and females did attack researchers at the nest when nestlings were being handled. The female was generally more aggressive, although both sexes attacked the researcher, often in tandem. The attacks were accompanied with alarm calls and contact was sometimes made to the head of the researcher. One female misjudged her attack and struck the researcher in the chest, and was subsequently captured for banding and blood collection. Some hawks stopped after a few attacks and then perched nearby (3-10m), alarm calling continuously, while others continued to attack for the entire 10-15 minutes that the researcher was at the nest.

Palmchats and Ridgway's Hawks nested in close association, with hawk nests being placed on top of the platform provided by Palmchat nests. Although Palmchats alarm called whenever Ridgway's left or returned to the nest, they did not abandon their colonial nest structure. Palmchats were observed adding nest material or perched within 1m of attending females, with neither bird showing much outward interest or concern. The remains of

Palmchats were found in seven hawk nests so although Ridgway's will predate Palmchats, it is not common. Ridgway's hawk appear to be more adapted to catching herptile than avian prey (Chapter 5).

Chapter 5

FEEDING ECOLOGY AND DIET

5.1 INTRODUCTION

Research on food provisioning at nests can provide information on limiting ecological factors within a species' environment. Food provisioning rates are generally a reliable index of prey availability (Newton 1979, Collopy 1984) and prey availability is one of the most significant factors affecting nest productivity in raptors (Newton 1979, Cook et al. 2003). Many aspects of a raptors' ecology are influenced by prey availability including adult nest attendance, foraging times, space use, and nestling growth and survival (Newton 1979, Turner et al. 2008, Dykstra et al. 2008).

Ridgway's Hawk is a forest raptor endemic to Hispaniola. It was locally common in areas of Haiti and the Dominican Republic at the turn of the century (Cory 1885, Wetmore & Lincoln 1934). The species is now limited to a small area of karst rainforest within Los Haitises National Park on the northeast coast of the Dominican Republic (Chapter 3). Reasons for the rapid decline are not fully understood, but forest loss and human persecution are likely to be major factors. Nearly all of the original forest cover is gone from Haiti, and 90% of the Dominican Republic's forests have been lost (Latta et al. 2006). Although Ridgway's Hawk does appear somewhat flexible in its use of different forest types (Chapter

3), it is clear that it requires some form of forest cover in order to survive. The productivity and survival of the species may be related to prey abundance within original forest habitats. Prey availability can affect a wide range of ecological characteristics for raptors, including population distribution and species viability (Newton 1979, Cully 1991). Improved understanding of the feeding ecology of Ridgway's Hawk, within an integrated study of territory use and breeding ecology, is required to determine which factors linked to loss of forest cover may be responsible for the rapid decline of this species.

Information on the diet of Ridgway's Hawk has been limited to museum specimen tags and observations on three breeding pairs in 1976 by Wiley & Wiley (1981). This chapter details the taxonomic composition and delivery rates and biomass of prey items at 22 Ridgway's Hawk nests monitored from 2005-2009.

5.2 MATERIALS AND METHODS

Breeding pairs of *Buteo ridgwayi* were studied over five breeding seasons (January to July 2005-2009 within Los Haitises National Park on the northeast coast of Hispaniola (see Chapter 2). General methods used to find and monitor breeding pairs are detailed in Chapter 2.

Detailed observations were carried out at six nests in 2005 and 2007, and five nests in 2006 and 2008 (Table 5.1). Nest sites were classified by the three main macrohabitat types within the study area (see Chapter 4):

1. Secondary forest;

2. New *conucos* ≤2 years old and;

3. Old *conucos* >2 years old.

Nest observations were carried out during standardized 4-hr observation sessions. Nests were each observed 2-6 times, from the time of hatching until fledging. If a nest failed earlier than fledging, the data collected up to that point was still included in the prey delivery and biomass analysis. Observations were carried out at multiple nests each year to minimize bias from territory location, macro-habitat, or individual bird/pair prey preference, and over multiple years to minimize bias from annual variation.

Food provisioning rates were examined by recording number of items delivered per 4-hr observation and the estimated the amount of biomass delivered. All prey deliveries were recorded by taxon and size class. Identification to at least genus was usually possible. Prey was also categorized into two size classes: small-average (<15cm) and medium-large (>15cm).

5.2.1 Data summary and analyses

Nestling ages were categorized by week: Week 1 = nestling 0-6 days old; up to Week 7 = 42-49 days.

Prey item biomasses are presented in Appendix 5.1. Mass estimates were based on field measurements of prey items captured within the study area and measured by the author, and from the literature (Wiley & Wiley 1981). When a prey item could only be identified to taxon group (e.g. unknown lizard), the average mass for items within that group was used.

Food provisioning rates were measured as number of food items delivered/nest/4-hr observation and biomass delivered/nest/4-hr observation. Total food provisioning rates were calculated for each nest and compared among years, and between successful and unsuccessful nests using ANOVA. A full factorial ANOVA compared food provisioning rates among nestling age and brood size.

Prey taxonomic composition recorded within the three macrohabitat types were compared using a Chi-square test. The *Scolopendra* records were not included in the analysis because sample size was too small (n=4). When distribution of prey types differed, Bonferroni Z-tests were used to examine which prey types were recorded more or less often than expected within the three macrohabitat types. Prey items recorded during nest observations in 2009 were included in prey taxa composition data. Standardized 4-hour nest watches could not be carried out in 2009 due to limited resources, and were therefore not included in delivery or biomass rate analyses.

5.3 RESULTS

The total number of observation hours was 344, consisting of eighty-six 4-hour sessions over a 4-year period. These observations were carried out on 22 nests (15.6h/nest, range 8-28 hr). A total of 390 prey items was delivered to nests during the study period, 362 of which were identified to taxa group: mammal, bird, lizard, snake, frog, or arthropod (Table 5.2). The prey item during 28 food passes could not be identified due to an obstructed view.

These deliveries were included in the analysis of number of items delivered per 4-hr observation, but were not included in the prey taxonomic composition analysis.

5.3.1 Prey taxa

Prey taxa delivered to nests by adult Ridgway's Hawk included lizards, snakes, birds, mammals, frogs and centipedes. Lizards (skinks and anoles) made up the largest percentage of prey items at 65.4% (Table 5.2). Snakes (tree snakes and false boas) made up the second largest percentage at 14.3%. Reptiles therefore accounted for 79.7% of all prey items brought to Ridgway's Hawk nests (Table 5.2). One genus of skink, *Celestus*, accounted for 33.1% of all prey items. Small mammals made up 9.1% of food items, followed by birds (5.5%), amphibians (4.4%), and centipedes at 1.1% (Table 5.2).

Lizards also made up the largest percentage biomass of prey items delivered to Ridgway's Hawk nests at 50.9% (Table 5.2). Snake biomass was estimated at 17.8%, for a total of 68.7% of the biomass of prey items consisting of reptiles (Table 5.2). Small mammals accounted for 18.1% of the biomass of prey items delivered to nests. Biomass of birds (10.8%), frogs (2.4%) and centipedes (0.4%) was less.

5.3.2 Prey items and biomass delivery rates

Over the study period, number of prey items delivered averaged 3.1 ± 1.2 per nest per 4-hr observation period. Food biomass delivered to nestlings averaged 103.1 ± 20.6 g per nest per 4-hr session (n=22 nests). Food provisioning rates did not vary among years (number of items: $F_{3,18}= 0.59$, $p= 0.62$; biomass: $F_{3,18}=0.39$, $p= 0.76$) or between successful and unsuccessful nests (number of items: $F_{1,20}$=.01, p=0.97; biomass: $F_{1,20}$=1.96, p=0.19).

Number of prey items delivered varied with age of the nestling(s) (Table 5.3). Nestlings aged 3 to 5 weeks received significantly more items than nestlings 1,2,6 and 7 weeks old (Fig 5.1). Number of prey items delivered did not vary with brood size (Table 5.3). Biomass delivered was significantly higher for nestlings 5 weeks old compared to all other weeks (Table 5.3, Figure 5.1). Biomass delivered did not vary with brood size (Table 5.3).

Prey taxonomic composition delivered did not vary with year (χ^2_3=4.43, p= 0.23) or nest site macro-habitat (χ^2_2=0.17, p= 0.87).

5.4 DISCUSSION

5.4.1 Prey taxa

Historical information on Ridgway's Hawk diet recorded in the literature and museum specimen tags included lizards (n=10), birds (3), and small mammals (3) (see Wiley & Wiley 1981). Observations of two pairs of Ridgway's Hawk during the breeding season of 1976, documented reptiles (lizards and snakes) comprising 56.0% of the number of prey items and 38.3% of prey biomass delivered to the nests (Wiley & Wiley 1981). Small mammals (rats and bats) were the most important prey taxa in terms of biomass (48.1%).

Lizards (*Celestus* and *Anolis*) made up nearly two-thirds (65.5%) of the prey items delivered to the 22 Ridgway's Hawk nests during the present study. Together with snakes (14.4%), reptiles comprised 79.9% of prey items and 68.3% of biomass delivered to nests. The genus

Celestus was particularly important representing 34.7% of prey items and 21.5% of prey biomass delivered to nests.

Small terrestrial mammals were important to the diet representing 9.1% of prey items and 18.1% of biomass delivered to nests, but not in as high a proportion as that recorded by Wiley & Wiley (1981). Similarly, birds, bats and frogs were part of the diet but in different relative proportions than those recorded by Wiley & Wiley (1981). The giant centipede *Scolopendra gigantea* and downy chickens *Gallus gallus domesticus* were recorded for the first time as part of the diet of Ridgway's Hawk. In both cases, single pairs were involved. All of the other 21 pairs had easy access to downy chickens within their territories. Countless observations have been made of Ridgway's Hawk hunting and ignoring downy chickens. It would appear that predation on downy chickens is an extreme rarity in Ridgway's Hawk but one that could cause irreparable damage to the species' reputation and survival.

The lizard genera recorded in historical records, *Leiocephalus* and *Ameiva,* are terrestrial lizards similar in size and habits to *Celestus* (author per. obs.), but are associated with more open scrub dry forests. Ridgway's Hawk may be relatively adaptable to different prey species, as long as reptile prey are available.

Prey items delivered to nests of the Puerto Rican Broad-winged Hawk *Buteo platypterus brunnescens*, the geographically closest forest *Buteo,* are similar to *B. ridgwayi* but proportions within the diet are different (Hengstenberg & Vilella 2005). The Puerto Rican

Broad-winged Hawk relies much more on rats (35% of diet) and birds (17%), and much less on snakes (3%). Lizards (primarily *Anolis* spp.) are an important component of the diet with 27% of prey items, but still not nearly as important as they are to Ridgway's Hawk.

With reptiles as such an important part of Ridgway's Hawk nestling diet, it is not surprising that the species has persisted in the wet lowland forests of Los Haitises. Los Haitises National Park supports some of the highest reptile diversities on the island, both in terms of abundance and species richness (Glor et al. 2001). In particular, the mogote hilltops support a particularly high diversity and abundance of lizard, and serve as refuges for species that can not tolerate habitat disturbance (Glor et al. 2001). This reliance on reptiles for feeding nestlings may also explain why Ridgway's Hawk are not found in any of the remaining undisturbed higher elevation forests, and why historical sightings of Ridgway's hawk > 550m asl were very rare. The higher elevation forests are much cooler and support depauperate reptile communities, in terms of both abundance and diversity (author pers. obs). These forests do support large numbers of small mammals, primarily introduced Ship Rats *Rattus rattus*, and native birds. Sharp-shinned Hawks *Accipiter striatus striatus* and Red-tailed Hawks *Buteo jamaicensis jamaicensis*, both adept hunters of birds and small mammals, were commonly seen in the higher elevation montane pine and broadleaf forests of the Sierra de Bahoruco, Cordillera Central, Cordillera Septentrional, and Cordillera Oriental (author pers obs.)

Although Ridgway's Hawk are somewhat flexible in their prey use, the last remaining population in Los Haitises are clearly relying on the abundant reptile populations in the karst rainforest for the majority of prey items delivered to nestlings.

5.4.2 Food provisioning

Delivery of food items to Ridgway's Hawk nestlings averaged 3.2 items per 4-hour observation. For the closely related Red-shouldered Hawk *B. lineatus*, prey delivery rates were very similar at 3.4 prey items delivered per 4-hr observation period (Dykstra et al. 2003). Biomass delivered to *B. ridgwayi* nestlings (103g) was slightly lower than biomass delivered to *B. lineatus* nestlings (116g) per 4-hr observation period. This is not unexpected as the body mass of *B. lineatus* is *c.*80% greater than *B. ridgwayi*. Wiley & Wiley 1981 also documented that the amount of food delivered to Ridgway's Hawk nests was lower than for the larger *B. lineatus* (Snyder & Wiley 1976). The Puerto Rican Broad-winged Hawk was found to have a mean prey delivery rate of 0.38 prey items per chick per hour, with a range of 0.14-0.80. This provisioning rate is somewhat lower than that of Ridgway's Hawk, but may be explained by the fact that larger prey items such as *Rattus* spp. comprised a greater part of the diet of the Broad-winged Hawk on Puerto Rico.

Prey availability can be an important indicator of habitat quality for raptors, and prey delivery rates are generally a reliable index of a habitat's prey base (Newton 1979). Breeding pairs nesting in suboptimal habitat with low prey availability tend to have lower prey delivery rates resulting in nestling mortality and lower adult productivity (Dykstra et al. 1998). Low food provisioning rates may also be an indicator of poor habitat quality. In the absence of historical information on Ridgway's Hawk food provisioning rates, it is difficult to assess this quantitative information with no baseline. However several results from this study suggest that the current food provisioning rates are representative of satisfactory levels of food availability. Firstly, food provisioning rates did not vary between successful or failed nests suggesting that food was not a limiting factor in nest outcome. This was also supported by the results of the nest success research (Chapter 4), which documented no instances of nest failure due to starvation. Secondly, excess food items were recorded at most nests during observations. Wiley & Wiley (1981) also noted uneaten food at nest sites and also reported that food appeared to be in ample supply.

Prey delivery and nestling provisioning rates in raptors has been shown to vary across the nestling growth period (Giovanni et al. 2007), as was found for the present study. Ridgway's Hawk adults delivered significantly more prey items to nestlings aged 3 to 5 weeks old, and significantly greater biomass to nestlings aged 5 weeks old. Similar results were documented for both Swainson's Hawk *B. swainsoni* and Ferruginous Hawk *Buteo regalis* (Giovanni et al. 2007) with the highest number of food items delivered to *B. swainsoni* nestlings at 5 to 6 weeks old, and to *B. regalis* nestlings at 3 to 4 weeks old. However, there was no correlation found between number of prey items delivered and age of nestlings for the Red-shouldered Hawk, Ridgway's Hawk's nearest taxonomic relative (Dykstra et al. 2003).

Food provisioning to *B. ridgwayi* nestlings was not correlated to brood size. This seems to be a fairly common phenomenon in hawks, including *Buteo* species, as recent studies have also found no correlation between food provisioning and brood size (*B. lineatus* in Dykstra et al. 2003; *B. swainsoni* and *B. regalis* in Giovanni et al. 2007; *Falco peregrinus* in Palmer et al. 2004; *Accipiter gentilis* in Smithers et al. 2005).

Prey taxonomic composition delivered to nests did not vary with macro-habitat of nesting sites. This may be explained by several scenarios. Firstly, small agricultural plots (*conucos*) are numerous and dispersed throughout the study area. Most Ridgway's Hawk territories now consist of a mosaic of habitat types, including newly cut and burned farmland in valleys next to older *conucos* with some regeneration adjacent to secondary forest on hilltops. A pair that is nesting in a valley with secondary forest, may also be hunting in surrounding valleys and hilltops with different macro-habitat types. Secondly, although it is assumed that more reptiles would be found in intact secondary forest, there has as of yet been no research carried out to discover if this is indeed the case. There may be adequate hunting opportunities for Ridgway's Hawk of terrestrial reptiles, such as skinks, within more fragmented open habitats adjacent to intact forest.

5.4.3 Conclusions

Ridgway's Hawk relies on reptiles for a large part of its diet, more so even than suggested by previous information. This explains in part the species distribution within low to mid-elevation forests, and why Ridgway's Hawk are not found in higher elevation forests, like the Sierra de Bahorucos, which still contain large areas of undisturbed forest. This reliance on an abundant prey base of reptiles can be considered a factor in the decline and rarity of Ridgway's Hawk.

The results of the food provisioning research suggest an abundant prey-base for the last population of Ridgway’s Hawk within Los Haitises National Park. The food provisioning data collected over the 5 years can serve as baseline information for future research, and for the management of captive birds. Reptile abundance should be considered an important habitat component when deciding on conservation strategies for the species, including potential areas for either translocations or releases of birds within their historical range.

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Table 5.1 Nest site information, hours of observation, and fates of nests monitored for Ridgway's Hawk from 2005-2008 SF = Secondary forest, OC= Old *conuco* > 2 years old, NC= New *conuco* ≤ 2 years old

Year	Nest ID / Macrohabitat*	No. of hours of observation	Age of nestlings (weeks)	No. of fledglings (No. of nestlings)
2005	Casa Grande-Carlos / SF	28	1-7	3 (3)
2005	Mata de Limones-Antonio / SF	24	1-3, 5-7	2 (2)
2005	Cacata-Ramon / SF	8	1-2	0 (2) [a]
2005	Cacatona-Bienbenidos / OC	20	2-6	2 (2)
2005	Britos-Benito / OC	12	1-3	0 (2) [b]
2005	Mata de Limones-Lico / SF	16	2, 4, 6-7	1 (1)
2006	Cacata-Pedro / SF	24	2-7	2 (2)
2006	Casa Grande-Renaldo / OC	16	1-4	0 (1) [c]
2006	Pueblo-Modeto / SF	12	3, 4, 7	1 (1)
2006	Arrolitos-Santo Marto / NC	8	2-3	0 (1) [d]
2006	Mata de Limones-Pilar / NC	12	1, 3, 6	2 (2)
2007	Pueblo-Modeto / NC	12	1-2	0 (1) [a]
2007	Arrolitos-Juan / OC	16	2-5	0 (3) [e]
2007	Aguatico-Sariano / OC	16	4-7	2 (2)
2007	Britos-Sierra / SF	12	3-5	0 (2) [f]
2007	Cacata-Ramon / NC	20	2-7	2 (2)
2007	Pueblo-Plinio / OC	12	2-5	2 (2)
2008	Britos-Balon / NC	8	1-2	0 (2) [a]
2008	Cacata-Damasa / OC	20	2-3, 5-7	1 (1)
2008	Mata de Limones-Nolo / NC	16	4-7	1 (1)
2008	Cacata-Miami / OC	16	3-4, 5,7	1 (2)
2008	Pueblo-Beato / SF	16	2-3, 5,7	2 (2)

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[a] unknown failure with young nestlings
[b] rocks found in nest, nestlings killed
[c] failed, rocks thrown at nest, nestling missing
[d] nestlings died of botfly infestation
[e] older healthy nestlings all died around same time, cause unknown, remains found intact in nest, excessive prey items at nest
[f] older nestlings eaten by villagers

Table 5.2 Prey delivered to Ridgway's Hawk nestlings from 2005-2008. Taxonomic group totals are in bold.

Prey item taxa	Number of items (% of total)	Biomass in g (% of total)
Lizards	**237 (65.5)**	**6390.7 (50.9)**
Anolis baleatus	38 (10.5)	1432.2
Anolis spp.	52 (14.5)	1573.0
Celestus spp. [a]	126 (34.7)	2690.4
Unidentified lizard	21 (5.7)	695.1
Snakes	**52 (14.4)**	**2231.9 (17.8)**
Uromacer spp. [b]	27 (7.4)	1379.7
Boas [c]	19 (5.3)	610.6
Unidentified snake	6 (1.6)	306.6
Mammals	**33 (9.1)**	**2284.4 (18.1)**
Rattus spp.	31 (8.5)	2244.4
Unidentified bat	1 (<0.3)	25
Unidentified rodent	1 (<0.3)	15
Amphibians	**16 (4.4)**	**296 (2.4)**
Eleutherodactylus spp.	16 (4.4)	296
Birds [a]	**20 (5.5)**	**1355 (10.8)**
Dulus dominicus	8 (2.2)	320
Saurothera longirostris	5 (1.4)	570
Unidentified passerine	2 (0.5)	50
Gallus gallus domesticus chick	2 (0.5)	90
Phaenicophilus palmarum	1 (<0.3)	60
Columba spp.	1 (<0.3)	220
Melanerpes striatus	1 (<0.3)	45
Arthropod	**4 (1.1)**	**48 (<0.4)**
Scolopendra spp.	4 (1.1)	48
Total	**362**	**12,563.5**

[a] *Celestus costatus* and *C. stenurus*, [b] *Uromacer catesbyi* and *U. oxyrhyncus*

[c] *Epicrates fordii* and *Tropodophis haetianus*

Table 5.3 The effect of nestling age and brood size on food provisioning rates of Ridgway's Hawk. (A - Number of prey items delivered and B - Biomass delivered).

A - Dependent Variable: Number of prey items delivered

Source	Type III SS	df	F	P
Nestling age	24.576	6	7.697	0.000
Brood size	0.858	2	0.807	0.453
Nestling age*Brood size	8.115	7	1.179	0.107
Error	37.248	70	0.532	

B - Dependent Variable: Biomass delivered

Source	Type III SS	df	F	P
Nestling age	8307.362	6	3.776	0.003
Brood size	43.578	2	0.059	0.942
Nestling age *Brood size	921.942	7	0.359	0.923
Error	25665.579	70		

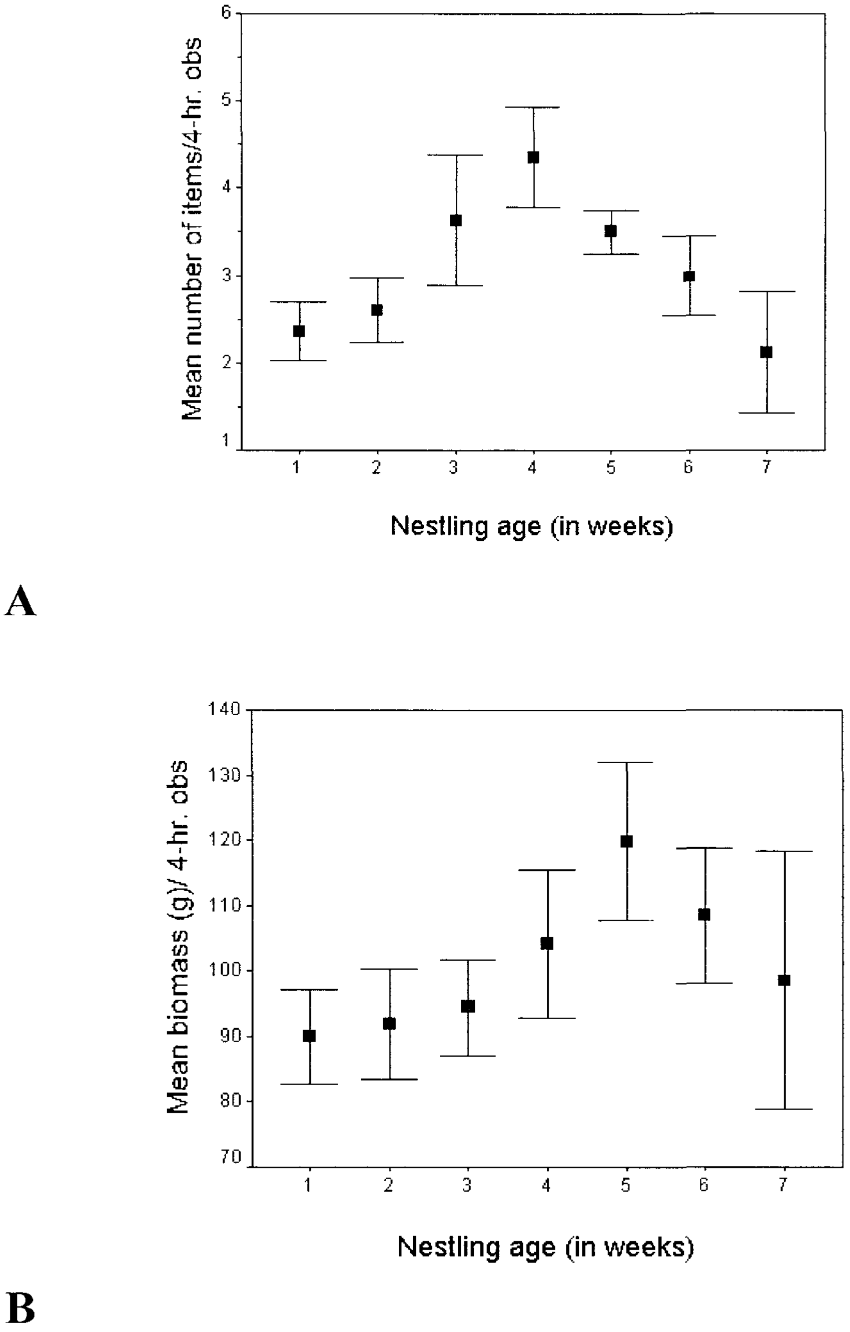

Figure 5.1 Food provisioning by adult Ridgway's Hawks as a function of nestling age. (A) Mean number of items delivered per 4-hr observation period. (B) Mean biomass of prey delivered per 4-hr observation period.

APPENDIX 5.1 Ridgway's Hawk prey item biomass. Measurements were from live animals captured by the author in the Dominican Republic, dead specimens collected from Ridgway's Hawk nests, or estimated from references from the literature.

Prey Item	Size Class	Mean Weight (g)	Sample size
Snakes			
Uromacer spp.	Small	23.7	11
	Large	51.1	13
Tropodophis haetianus	Small	32.8	7
	Large	68.2	6
Epicrates fordi	Small	24.3	5
	Large	56.8	3
Unidentified snake	Small	26.9	(mean of above snake spp)
	Large	58.7	(mean of above snake spp)
Lizards			
Anolis spp.	Small	17.4	11
Anolis baleatus	Large	43.1	15
Celestus spp.	Small	10.2	13
	Large	27.0	10
Unidentified lizard	Small	13.8	(mean of above lizard spp)
	Large	37.2	(mean of above lizard spp)
Mammals			
Rattus spp.	Large	72.4	5
Unidentified bat	Small	25	estimate
Unidentified rodent	Small	15	estimate
Amphibians			
Eleutherodactylus spp.	Small	18.5	3
Birds			
Dulus dominicus		40	1
Saurothera longirostris		114	2
Columba spp.		220	1
Melanerpes striatus		45	3
Phaenicophelus palmarum		60	2
Gallus gallus domesticus chick		45	2
Unidentified small passerine		25	estimate
Arthropod			
Scolopendra spp.		12g	2

Chapter 6

GENETIC DIVERSITY AND STRUCTURE OF THE REMAINING POPULATION

6.1 INTRODUCTION

Island avian populations have a higher risk of extinction than mainland populations (Myers 1979, Smith et al. 1993). Ninety percent of bird extinctions in historic times have been on islands (Myers 1979). Susceptibility of island birds to extinction is primarily related to human induced change through habitat loss, persecution, and introduction of exotic species (Olson 1989 cited in Frankham 1997, Pimm et al. 2006, Boyson 2010), in combination with genetic factors (Frankham 1998, Frankham 2005). Initial susceptibility of populations to extinction can be predicted by genetics (Frankham 1995a), with factors such as inbreeding (Frankham 1995b) and mutational meltdown (Lynch et al. 1995) leading to genetic deterioration and increased extinction risk.

Genetic variation has been examined in widespread mainland bird species (Mock et al. 2002, Caizergues et al. 2003, Van Den Bussche et al. 2003, Godoy et al. 2004, Martinez-Cruz et al. 2004), and isolated island endemics (Ardern & Lambert 1997, Tarr et al. 1998, Tarr & Fleischer 1999, Boessenkool et al. 2007, Groombridge et al. 2000, 2009). In general, island endemic species exhibit lower genetic variation than mainland populations (Frankham

1997). Allelic richness and heterozygosity have been lower in smaller, isolated fragmented populations with reduced gene flow and increased genetic drift, than in larger more diverse populations of the same species (Johnson et al. 2004, Martinez-Cruz et al. 2004, Bollmer et al. 2005, Huang et al. 2005). Molecular research has also supported the hypothesis of lower genetic variability in endemic vs. migratory island species, and in island vs. continental species (Frankham 1997, Zwartjes 2003, Boessenkool et al. 2007), indicating lower effective population sizes on islands.

Population status has also been shown to be associated with genetic diversity (Johnson & Stattersfield 1990). An analysis of 170 pairs of threatened and related non-threatened taxa revealed that mean heterozygosity was 35% lower for the threatened counterparts (Spielman et al. 2004). Evan & Sheddon (2008) examined correlates of genetic diversity with respect to conservation status in 194 bird species and found a significant decline in mean heterozygosity with increasing extinction risk. The authors concluded that the smaller populations of threatened species were largely responsible for this relationship.

The restricted range, small population size, and threatened status of Ridgway's Hawk make it very vulnerable to the general underlying patterns of small population genetics. Fluctuations in effective population sizes, genetic drift, and reduced gene flow in small, isolated populations can result in reduced genetic variation and inbreeding depression (Hedrick & Kalinowski 2000, Keller & Waller 2002). This can lead to a greater risk of extinction due to lower fitness and lack of ability to adapt to rapid changes in environmental conditions (Frankham 1995a, Reed 2003, Bolund et al. 2010). Most populations are impacted by genetic factors before they are driven to extinction (Spielman et al. 2004, Frankham 2005).

One of the top priorities in conservation genetics is to 'institute rational genetic management of threatened species in the wild', especially for small fragmented populations (Frankham 2010). If genetic factors are not taken into account, extinction risks may be underestimated and inapplicable recovery strategies implemented (Frankham 2005, 2010). The present study examines the genetic diversity and structure of the small, declining Ridgway's Hawk population to assess the potential risks of extinction from genetic factors to incorporate these findings within an appropriate conservation strategy.

6.2 METHODS

Breeding pairs of *Buteo ridgwayi* were studied over five breeding seasons (January to July 2005-2009 within Los Haitises National Park on the northeast coast of Hispaniola (see Chapter 2). Methodology for breeding pair monitoring, DNA collection and extraction are detailed in Chapter 2.

6.2.1 Microsatellite genotyping

Fourteen microsatellite loci isolated from Common Buzzard *Buteo buteo* (Johnson et al. 2005) and Swainson's Hawk *Buteo swainsoni* (Hull et al. 2007) were used for examining allelic variation in *B. ridgwayi* (Table 6.1). Polymerase Chain Reaction (PCR) protocols for each set of primers were optimized for *B. ridgwayi* using blood from 24 individuals (6 adult females, 6 adult males, and 12 nestlings) sampled in 2005-2007. Non-radioactive, fluorescently-labelled (Black, Blue and Green) microsatellite primers were provided by Integrated DNA Technologies (IDT^{TM}). Optimal reagent volumes and annealing temperatures varied by primer sets. In general, genomic DNA was amplified for each individual in 10 ul reactions containing 5.3-6.4 ul distilled water, 1.0 ul of PCR reaction buffer (10X TSG), 0.6-1.4 ul of 20mM MgSO4, 0.4 ul of 10mM dNTPs, 0.2 ul of fluorescently dyed 10uM forward and reverse primers, 0.2 ul of Taq DNA polymerase (TSG), and 1ul of DNA template (*c.*15ng DNA in TE buffer). PCR reactions were carried out in an Eppendorf MasterCycler^{TM} thermal cycler.

For the Bbu primer pairs: An initial 2 minute denaturing step at 94°C was followed by 12 cycles of 45 s at 94°C, 45 s at the primer specific annealing temperature, and a 50 s extension step at 72°C. This was followed by a further 22 cycles of 30 s at 89°C, 45 s at the primer specific annealing temperature, and a 50 s extension step at 72°C. The PCR reaction finished with a final 5 minute extension step at 72°C, and samples were then held at 4°C until taken from the thermal cycler. Primer specific annealing temperatures were as follows: Bbu51 50°C, Bbu 17 and Bbu 34 53°C, Bbu46 54°C, Bbu42 55°C, Bbu03 56°C, Bbu33 58°C, and Bbu59 59°C. For the Bsw primer pairs (Bsw107, 122, 207, 234, 310 and 324): An initial 2 minute denaturing step at 94°C was followed by 30 cycles of 30 s at 94°C, 45 s at 58 An initial 2 minute denaturing step at 94°C was followed by 12 cycles of 45 s at 94°C, 45 s at 58°C, and a 45 s extension step at 72°C. This reaction finished with a 30 minute extension step at 72°C and PCR products were then held at 15°C until removed from the thermal cycler.

Each locus was amplified separately but since primers had been fluorescently labelled, loci were pooled post-PCR in Poolplex reactions. PCR products were visualized using a CEQ 8000^{TM} DNA sequencer, and allele sizes were assigned using the Beckman Coulter CEQ 8000 Genetic Analysis System^{TM} software.

6.2.2 Data analysis

All genotype data was run through MICRO-CHECKER (Van Oosterhout et al. 2004, 2006) to check for typographical errors, scoring errors (large allele drop-out and stuttering), and the presence of null alleles.

6.2.2.1 Genetic diversity

The observed heterozygosity, expected heterozygosity, and number of alleles were calculated using ARLEQUIN software Version 3.1 (Excoffier et al. 2005). Tests of Hardy–Weinberg equilibrium (HWE) and linkage disequilibrium (LD) were completed in GENEPOP Version 4.1.10 (Rousset 2008). Linkage disequilibrium between all pairs of loci and tests for deviation from HWE were tested using a Markov exact test with 10,000 dememorization steps, 1,000 batches and 5,000 iterations per batch (Slatkin & Excoffier 1996, Guo & Thompson 1992). For both HWE and LD, a Bonferroni correction for multiple tests was implemented (Zar 1999). Significance for the HWE exact tests was set at $P<0.01$ following Barrett et al. (2005).

Allelic richness was calculated in FSTAT Version 2.9.3 (Goudet 2001), which accounts for variation in sample sizes. F_{IS} (inbreeding coefficient) was estimated in GENEPOP Version

4.1.10 (Rousset 2008) using the single locus estimates following a standard ANOVA (Weir & Cockerham 1984).

6.2.2.2 Population structure

A Bayesian approach was used to assess population structure to determine if any individual hawks could potentially be migrants from an undiscovered subpopulation. The program STRUCTURE Version 2.3 (Pritchard et al. 2000) was used to determine the number of subpopulations, K, with models for admixed ancestry and correlated allele frequencies (Falush et al. 2003). The program was run for values of K = 1 through 10. An initial burn-in of 10,000 iterations was followed by a subsequent run of 100,000 iterations. Analysis with this parameter set was performed 10 times and the log Pr (X/K) statistic averaged across runs. Based upon the preliminary results, which showed a clear drop off after K=1, a second parameter set was run for fewer K values (1 through 5). This was also run using admixture and correlated allele frequency models, a burn-in of 100,000 iterations, and a run length of 1,000,000 iterations. The log Pr (X/K) statistic was averaged across 10 runs.

To test for an imprint of a recent genetic bottleneck, both Sign and Wilcox sign tests were carried out in the program BOTTLENECK Version 1.2.02 (Cornuet & Luikart 1996; Piry et al. 1999). Field-tests have shown this program to be accurate in detecting signatures of a population bottleneck (Cristescu et al. 2010). Analyses used the strict infinite allele model (IAM) and a two-phase model (TPM) approach of microsatellite mutation (Di Rienzo et al. 1994). The TPM allows a user to specify a proportion of the step-wise mutation model

(SMM) used in a multi-step model. TPM analysis was done with default settings.

6.2.2.3 Effective population size (N_e)

Effective population size (N_e) is defined as the size of an ideal population that has the same rate of change in heterozygosity as the observed population (Wright 1931). It is a measure of the rate of genetic drift, related to the loss of genetic diversity and the rate of increased inbreeding within a population (Wright 1969 cited in Reiman & Allendorf 2001). N_e is estimated either genetically using F-statistics and coefficients of inbreeding, or demographically in terms how many individuals actually contribute to the breeding population. Genetic estimates of N_e generally assume non-overlapping generations (Barton & Whitlock 1997, Hedrick 2005). The Ridgway's Hawk samples likely represent at least two overlapping generations during the study period, and this assumption would therefore be violated. However, the results of the analysis are still reported here. MIGRATE version 3.0 (Beerli & Felsenstein 1999, 2001; Beerli 2008) was used to estimate the parameter Theta (Θ) where Θ = 4 x effective population size (N_e) x mutation rate (u). Brownian motion approximation to the ladder model was used (Ohta & Kimura 1973), and equal mutation rates among loci were assumed. The program was run four times to check whether chains were estimating the same maximum-likelihood for Theta.

Demographically measured effective population size according to Frankham (1995c) is generally 1/10th the size of the censused population. This can be highly variable, but is generally an acceptable starting point for estimating N_e. Counts of breeding pairs can also be used to index N_e (Hedrick 2005). When not all pairs produce an equal number of offspring, N_e can be estimated as:

$$N_e = \frac{\mathbf{N}k - 1}{k - 1 + V_k / k}$$

Where (for this study) k is mean productivity measured as the number of young fledged per active nest over the study period, V_k is the variance in productivity per pair over the study period, and N is the count of breeding pairs estimated over the study period (as in equation 6.12b in Hedrick 2005).

6.3 RESULTS

Three of the *Buteo* loci tested were monomorphic in all individuals, and therefore not included in analyses. Loci *Bbu*59 was monomorphic for 135bp, *Bbu*03 for 205bp and *Bbu*17 for 170bp. The remaining 11 loci exhibited some variation.

6.3.1 Genetic diversity

The analyses revealed between 4 and 19 alleles, with an average of 9.4 ± 4.1 alleles per locus (Table 6.2). Allele frequencies ranged from 0.0069 to 0.4960 (Table 6.3). All of the 11 loci exhibited at least one rare allele (frequency <5%), with 82% of loci exhibiting 2-5 rare alleles (Table 6.3). Within the 149 individual Ridgway's Hawks sampled, 20 of the 102 alleles appeared in five or fewer individuals, and 31 (30%) were found in 10 or fewer individuals (Table 6.3). Furthermore, three of these rare alleles (alleles 221 and 227 in locus *Bsw*107, allele 365 in locus *Bsw*122) were found only in non-breeding individuals that subsequently died.

Observed heterozygosity across loci ranged from 0.521 (*Bbu*33) to 0.884 (*Bsw*234), with a mean observed heterozygosity of 0.732 ± 0.135 (Table 6.2). Expected heterozygosity across loci ranged from 0.538 (*Bbu*33) to 0.922 (*Bsw*324), with a mean expected heterozygosity of 0.780 ± 0.106 (Table 6.2). Five of the loci exhibited significant deviations from Hardy-Weinberg equilibrium (Table 6.2) with 4 loci being heterozygote deficient (*Bbu*34, *Bsw*122, *Bsw*207 and *Bsw*324) and one locus exhibiting heterozygote excess (*Bsw*234). Deviations from Hardy-Weinberg equilibrium can suggest that the samples do not represent a panmictic population, or can indicate the presence of null alleles and/or scoring errors. None of the loci showed any evidence of scoring errors from stuttering or large allele dropout when analyzed in Micro-Checker. For three of the loci with significant deviations from HWE (*Bbu*34, *Bsw*122, and *Bsw*234) there was no evidence of null alleles. There was evidence of possible null alleles in *Bsw*207 and *Bsw*324, and therefore allele frequencies and genotypes were adjusted in Micro-Checker to account for this. After adjustment, there were still significant deviations from HWE in the locus *Bsw*324 ($p<0.00$), but not in *Bsw*207 ($p=0.59$, Table 6.2). After Bonferroni correction, there was evidence of linkage disequilibrium for 29 of the 55 pairwise combinations of loci (Table 6.4).

There was possible evidence of inbreeding within the sampled population of *B. ridgwayi*, as measured by the inbreeding coefficient (Table 6.2). Nine of the 11 loci exhibited F_{IS} values above zero indicating an excess of homozgyosity which is consistent with some level of inbreeding.

6.3.2 Population structure

Preliminary STRUCTURE analyses indicated that log Pr(X/K) declined sharply beyond $K = 1$, consequently the second parameter set focused on K values of 1–5. The second parameter set, averaged across 10 runs, again showed no geographic structure evident in the population and a graph of log Pr(X/K) peaked at $K = 1$ (Figure 6.1). These results suggest that the samples comprise a single genetic population.

Both tests for a recent signature of a bottleneck were significant. The analysis was carried out with all 11 loci, and also with only the 7 loci in HWE. The results were similarly significant for both data sets. A significant excess of heterozygotes was detected by both the Wilcoxon sign-rank test (for both data sets $P < 0.001$ IAM, $P < 0.001$ TPM) and also from the Sign Test (for both data sets $P<0.01$ IAM, $P<0.01$ TPM), indicating a recent substantial reduction in effective population size for *B. ridgwayi*.

6.3.3 Effective population size

The results from the genetic analysis are reported as Theta values in Table 6.2.

Demographic estimates of effective population size of *B. ridgwayi*, according to Frankham (1995c), were *c.*9-11 breeding pairs, based on 10% of the censused population estimate of 91-109 pairs (Chapter 3). Effective population size estimates according to Hedrick's equation were also very similar at 15-18 pairs; where mean productivity over the study period (k) = 0.64 (Chapter 4), variance per pair over the study period (V_k) = 2.89, and number of estimated breeding pairs (N) = 91 – 109.

The results for both these methods indicate an extremely low effective population size for the remnant population of *B. ridgwayi*.

6.4 DISCUSSION

6.4.1 Mean heterozygosity of Ridgway's Hawk compared to other avian taxa

Mean heterozygosity *of Buteo ridgwayi* (0.732) was similar with a range of mainland avian taxa, including passerines, seabirds, parrots and cuckoos (see Table 6.5). In raptors, studies of genetic diversity using microsatellite markers have generally reported lower heterozygosity than that found in Ridgway's Hawk; however, a few genetic studies have reported similar levels (Table 6.5). Threatened avian species, either insular or listed as 'Endangered' or 'Critical' by IUCN, are also generally reported to have lower heterozygosity than Ridgway's Hawk, for both non-raptors and for raptors (Table 6.5).

The most extreme cases of island raptor declines, the contemporary populations of Mauritius Kestrel *Falco punctatus* and Seychelles Kestrel *Falco araea* exhibit extremely low levels of heterozygosity: 0.100 and 0.104 respectively (Groombridge et al. 2000, 2009). Both these populations declined to a handful of individuals prior to population recovery (Groombridge et al. 2001, 2009).

In general, Ridgway's Hawk appear to exhibit relatively higher levels of heterozygosity relative to other avian species, even though the current effective population size estimate for Ridgway's Hawk is extremely low at ≤18 breeding pairs. However, comparisons of heterozygosity across studies, while prevalent in the literature (Spielman et al. 2004, Evan & Sheddon 2008) are somewhat ambiguous since there is a strong association between heterozygosity and microsatellite length, repeat motif, and mutation rate, and this can vary considerably among taxa (Neff & Gross 2001). Increased heterozygosity may be the result of longer microsatellite length or higher mutation rate.

The most applicable comparison of genetic diversity is obtained by comparing homologous loci. Within the genus *Buteo*, heterozygosity for Ridgway's Hawk appears to be greater than mainland populations of Common Buzzard *B. buteo* (0.53 in Johnson et al. 2005) and less than Swainson's Hawk *B. swainsoni* (0.82 in Hull et al. 2008). However, a comparison of the homologous loci from the two above species (from which the primers were developed) reveals that *B. ridgwayi* exhibits reduced levels of genetic diversity compared to both mainland species. Two homologous loci for which variability was tested on *B. buteo* (Bbu42 and Bbu46) exhibited higher levels of heterozygosity at 0.93 and 0.89, and higher levels of allelic diversity at 15 and 17 alleles per locus, compared to *B. ridgwayi* with heterozygosity of 0.79 and 0.82, and allelic diversity of 8 and 9 alleles per locus, respectively. Similarly, the six homologous loci from *B. swainsoni* showed both higher heterozygosity levels (0.91±0.04) and higher allelic diversity levels (18.5±8.7 alleles per locus) compared to *B. ridgwayi* (heterozygosity of 0.84±0.05; and allelic diversity of 11.4±4.0). These results show that *B. ridgwayi* has reduced allelic diversity and lower heterozygosity compared to mainland *Buteo* species.

The appearance of relatively higher levels of heterozygosity for *B. ridgwayi* relative to other avian species may be due to the fact that high levels of heterozygosity are expected for a species that has had a relatively large population size until recently, with heterozygosity decreasing slowly after a bottleneck depending on the N_e (Wright 1931). In addition, a recent bottleneck can also temporarily elevate levels of heterozygosity (Nei et al. 1975). Heterozygosity is reduced more slowly than allelic diversity in populations that have recently experienced a considerable reduction in effective population size, and observed heterozygosity tends to be greater than expected from the observed allele number at mutation-drift equilibrium (Luikart et al. 1998). This results in transient elevated levels of heterozygosity, while in fact the actual heterozygosity may be considerably lower.

6.4.2 Heterozygote excess or deficiency in Ridgway's Hawk?

Heterozygote deficiency was significant in four of the 11 loci, and close to significant for 2 additional loci. This could be caused by sex-linked loci, presence of null alleles, population structuring or inbreeding (Wattier et al. 1998).

If heterozygote deficit loci were situated on the Z chromosome, females (ZW) would be hemizygous and appear to have excess homozygotes. If heterozygote deficit loci were on the W chromosome, females would be homozygous and the males (ZZ) would not have amplified. In the present study, heterozygosity was observed for both males and females in all 11 loci, and all individuals amplified, indicating that none of the loci were sex-linked.

Null alleles are more common if the source species for the locus is different from that of the tested species, which was the case for this study. However, only 2 loci, *Bsw*207 and *Bsw*324 exhibited evidence for the presence of null alleles. After adjusting genotypic and allele frequencies, there was still significant deviation from HWE in *Bsw*324 suggesting that the source of the deviation for this locus was not from null alleles. *Bsw*207 was in HWE with adjusted frequencies suggesting that null alleles were likely present for that one locus. Excess homozygosity can only be attributed to null alleles in this one instance.

Another potential cause of excess homozygosity is population structuring. The analysis of the population structure of Ridgway's hawk revealed one genetically similar population, with no evidence of hidden structure. Therefore, it is highly improbable that the excess homozygosity observed within this study was due to substructuring within the population.

The HWE significance was intentionally set at $P<0.01$ following Barrett et al. (2005), rather than the standard $P<0.05$. This was done in recognition of small disturbed populations violating the assumptions of HWE, which include an effectively infinite population size and non-random mating (Hardy 1908). Even with increased sensitivity, four loci deviated significantly from HWE. With a significance level set at $P<0.05$, seven of the 11 loci would have deviated from equilibrium, with 2 others close to significant deviation. A deviation from HWE at one or two loci may occur because of natural selection. However, deviations from HWE at many loci are an indicator of population structuring or non-random matins (Guo & Thompson 1992). Since the population structure analysis revealed no structuring, this strongly suggests that the Ridgway's Hawk samples do not represent a panmictic population, and that inbreeding is occurring.

Further evidence for inbreeding is provided by several other aspects of the genetic research including results of the linkage disequilibrium analysis. Linkage disequilibrium refers to the non-independence of alleles at different loci. This manifests as allele combinations occurring more often across loci than expected by chance, based on their respective frequencies in the population (Gaut & Long 2003). LD can be caused by new mutations, interbreeding of genetically divergent populations, inbreeding, and population bottlenecks. LD can be lost more quickly in larger populations than in smaller ones (Epperson & Allard 1987; Gaut & Long 2003). In the Ridgway's Hawk samples, LD was significant between 29 of the 55 loci pairwise combinations. This represents a substantial amount of linkage and most likely reflects inbreeding occurring within the population. This could also be the result of the recent bottleneck experienced by the population, or by some combination of the two.

The inbreeding coefficient (F_{IS}) also suggested excess homozygosity in several loci. F_{IS} measures the difference between observed and expected heterozygosity. F_{IS} values range from –1 to +1 and indicate either heterozygote excess (outbreeding) with negative values, or heterozygote deficiency (inbreeding) with positive values. Nine of the 11 F_{IS} values reported in this study were > 0 which is considerable given that with random matings the expected values would be 0.

Inbreeding is a demographic scenario that affects the entire genome, and given that many loci deviate from HWE and exhibit LD and almost all F_{IS} values are positive, there is strong genetic evidence of inbreeding occurring within the population.

The apparently conflicting result of excess homozygosity in 4 loci, yet relatively high levels of heterozygosity, may be explained by the fact that recent bottlenecks tend to primarily affect alleles that occur at low frequencies, and can result in transient elevated levels of heterozygosity due to a drift in allele frequencies (Nei et al. 1975). Therefore, levels of heterozygosity could be temporarily elevated from a recent genetic bottleneck, yet some loci could also be exhibiting excess homozygosity by means of inbreeding.

6.4.3 Allele frequencies in Ridgway's Hawk

The presence of numerous rare alleles in almost all loci is a cause for concern. Eighty-two percent of loci exhibited 2-5 rare alleles. Twenty percent of alleles were found in five or fewer individuals and 30% found in 10 or fewer individuals. Three rare alleles were found only in nestlings that subsequently died before fledging.

The effect of low frequency alleles in large populations is generally minimal, since <1% of the population may still potentially include >1000s of individuals that carry the allele. However, in small populations where only a handful of animals carry the allele, there would be a substantially greater risk of allele extinction.

Population bottlenecks can purge low frequency alleles from a population at a rapid rate. Bellinger et al. (2003) found a 29% loss (16/55) of alleles across six loci during a 50 year period in the Wisconsin population of Greater Prairie Chicken *Tympanuchus cupido*. The remaining small population of Ridgway's Hawk is at similar high risk of losing low frequency alleles. The 34 adults sampled during the current study could represent *c*.30% of the remaining breeding pairs of this species. Based on the results from this analysis, it is probable that 20-30% of alleles are found in only a small number of remaining adults and these have a high probability of being lost from the population. The fact that many low frequency alleles still exist in the population could also suggest that the population has not yet come through the bottleneck.

6.4.4 Effective population size (N_e)

The present study's preliminary analysis of effective population size, as measured demographically, suggests that the current population is losing genetic variation at a rate similar to that of a population with ~20-40 individuals. The generally accepted view is that any population with an $N_e<50$ is at serious risk of inbreeding depression. Although populations might occasionally decline to numbers on this order without adverse effects, maintenance of adaptive genetic variation over many generations generally requires a higher N_e (Reiman & Allendorf 2001).

6.4.5 Conclusions

Genetic diversity (heterozygosity) in Ridgway's Hawk appears to be relatively high for an insular threatened species with a low population size. This could be positive for the recovery of the species, if the current population decline is halted and the population is able to increase rapidly. Maximizing breeding contributions from as many adults as possible in the short-term, could capture much of the remaining genetic variation. The observed high levels of genetic diversity may also help Ridgway's Hawk adjust to environmental changes.

However, there are several results from the population genetic analysis that are cause for concern:

1) Analysis revealed evidence of a genetic bottleneck, representing a large decrease in effective population size. In addition, since allelic diversity is reduced faster than heterozygosity during bottlenecks, this results in transient elevated levels of heterozygosity. Therefore, heterozygosity of the population may be in fact much lower than this study reports.

2) Several loci exhibited both deviations from HWE (5 loci) and linkage disequilibrium (29 of 55 pairwise comparisons) indicating that inbreeding is occurring within the population. This was supported by positive F_{IS} values for 9 of 11 loci. Close inbreeding at a substantial rate is a potential concern in the future.

3) Thirty percent of alleles were present in 10 or fewer of the sampled individuals. This high frequency of rare alleles means that Ridgway's Hawk is still at serious risk of losing genetic variation due to drift.

4) Effective population size is very low, and the results suggest that the current population may be losing heterozygosity at a rate similar to a population with just 20-40 individuals.

The results of the current population genetics study can be used as a baseline for future population genetic research, and for wild and captive population management. It is understood that the current study represents only a preliminary analysis of population genetics for this species. Future research should compare the historical genetic diversity and structure, available as museum specimens, to the contemporary population. This would be useful in determining the rate of loss of genetic variation that has occurred within the population since the turn of the century, and whether Ridgway's Hawk has already experienced previous bottlenecks.

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Table 6.1 Microsatellite loci used to assay variation in *Buteo ridgwayi*.

Locus	Species	Motif	Accession No.	Primer sequence (5'-3')	PCR product size (bp) for *B. ridgwayi*	Reference
*Bbu*33	*Buteo buteo*	$(GT)_{12}$	AJ715903	F: TGCCGCCATCTTACTGAAG R: ATCACAAGATAGCCAGCTATGG	165-171	Johnson et al. 2005
*Bbu*34	*Buteo buteo*	$(AC)_{12}$	AJ715904	F: AGACCAGCAAACCCAAACAG R: TTGATATATCTTGCTCCATGCTG	155-162	Johnson et al. 2005
*Bbu*42	*Buteo buteo*	$(GGGT)_5(GA)_5$	AJ715912	F: GGGATAAGAATGCCAGAACTTG R: TGGGTGGCTAAATCTTGAGG	158-174	Johnson et al. 2005
*Bbu*46	*Buteo buteo*	$(AC)_{12}$	AJ715916	F: TGAACCCTGGAGAAAGATGC R: CAATTTGGGGAGACGTGATG	168-188	Johnson et al. 2005
*Bbu*51	*Buteo buteo*	$(AC)_{17}$	AJ715921	F: GACCTGGTGCTCTGCATTC R: TGAAACAGATTTGATTCTGGATG	154-170	Johnson et al. 2005
*Bsw*D107w	*Buteo swainsoni*	$(GAGAA)_{14}$	DQ985716	F: CCATCTCTTGGTCCTGTTT R: CTACAATCCTGTCTGGACATG	175-227	Hull et al. 2007
*Bsw*D122w	*Buteo swainsoni*	$(GAGAA)_{10}$	DQ985717	F: GTCAGGCAGTTGGACTAGATGA R: GATGGGGAACTGCTCTAAACAT	319-375	Hull et al. 2007
*Bsw*D207w	*Buteo swainsoni*	$(GAGAA)_{14}$	DQ985720	F: TGGGAAAAGTAGTTAGGAAGTG R: CTCAGCCAGTCTTGTTGTG	228-257	Hull et al. 2007
*Bsw*D234w	*Buteo swainsoni*	$(GAGAA)_{17}$	DQ988163	F: GGAATTGCATAGGTCAAACACA R: CTGTGCAACATATTATTTCCCTTG	219-192	Hull et al. 2007
*Bsw*D310w	*Buteo swainsoni*	$(GAGAA)_{24}$	DQ985725	F: GAACAATTTGGGATACACTGA R: TAATGCCATGATGTTATCAGAC	219-297	Hull et al. 2007
*Bsw*D324w	*Buteo swainsoni*	$(GAGAA)_{27}$	DQ985728	F: AAAAGGATTGAAGGAGTTGG R: CCCTGTTGTGCATCTTTG	317-421	Hull et al. 2007

Table 6.2 Polymorphism data for 11 microsatellite loci tested across *Buteo ridgwayi* samples. Data underlined are adjusted allele frequencies from Micro-Checker, accounting for possible null alleles.

Locus	**k**	**n**	**H_o**	**H_e**	**HW Pvalue**	**AR_C**	**F_{IS}**	**Θ**
*Bbu*33	4	142	0.521	0.538	0.054	4.00	0.0884	1.5403
*Bbu*34	4	135	0.585	0.617	**0.000***	4.00	0.1261	2.3620
*Bbu*42	8	147	0.789	0.799	0.087	7.99	0.0600	4.0453
*Bbu*46	9	142	0.873	0.823	0.133	8.98	-0.0113	5.2346
*Bbu*51	6	136	0.751	0.755	0.501	6.00	0.0138	2.8827
*Bsw*107	11	144	0.855	0.809	0.014	10.96	-0.0352	6.4703
*Bsw*122	12	139	0.771	0.828	**0.001***	11.00	0.1078	6.4545
*Bsw*207	8	142	0.640	0.783	**0.006***	8.00	0.1758	5.0631
*Bsw*207	8	119	0.764	0.790	0.592			
*Bsw*234	8	138	0.884	0.820	**0.001****	7.98	0.0918	5.6439
*Bsw*310	13	142	0.866	0.883	0.011	13.00	0.0655	6.7678
*Bsw*324	19	120	0.520	0.922	**0.000***	18.98	0.4163	13.10
*Bsw*324	19	100	0.880	0.920	**0.000***			
All loci	9.4	149	0.732	0.780	---	---	---	4.4927
SD	4.1		0.135	0.106				(4.3807 - 4.7289)

Total number of alleles (k), number of individuals typed (n), observed heterozygosity (H_o), expected heterozygosity (H_e), Hardy-Weinberg equilibrium exact test P-value (HW Pvalue) with significance of $P<0.01$, allelic richness corrected for sample size (AR_C), inbreeding coefficient (F_{IS}) and Theta (Θ). * Homozygous excess, ** Heterozygous excess.

Table 6.3 Microsatellite allele frequencies and counts for *Buteo ridgwayi*. For alleles with counts ≤ 10, the total number of sampled individuals with the corresponding allele is included in parentheses (n).

Loci	Allele	Count(n)	Frequency
***Bbu*33**	165	7 (7)	0 0246
	167	123	0 4331
	169	5 (4)	0 0176
	171	149	0 5246
***Bbu*34**	155	95	0 3519
	157	134	0 4963
	159	31	0 1148
	162	10 (8)	0 0370
***Bbu*42**	158	82	0 2789
	160	13	0 0442
	162	36	0 1224
	164	5 (5)	0 0170
	168	30	0 1020
	170	81	0 2755
	172	43	0 1463
	174	4 (3)	0 0136
***Bbu*51**	154	24	0 0882
	160	49	0 1801
	162	109	0 4007
	164	53	0 1949
	168	25	0 0919
	170	12	0 0441
***Bsw*310**	219	5 (5)	0 0176
	229	8 (8)	0 0282
	243	18	0 0634
	248	12	0 0423
	253	5 (5)	0 0176
	258	25	0 0880
	262	31	0 1092
	267	54	0 1901
	272	41	0 1444
	277	50	0 1761
	282	11	0 0387
	287	13	0 0458
	297	11	0 0387
***Bsw*234**	219	55	0 1876
	224	23	0 0870
	229	60	0 2174
	233	76	0 2754
	238	24	0 0870
	243	21	0 0761
	286	2 (2)	0 0072
	291	15	0 0543
***Bsw*122**	319	7 (7)	0 0252
	324	42	0 1511
	329	93	0 3345
	334	23	0 0827
	339	25	0 0899
	345	5 (5)	0 0180
	350	21	0 0755
	355	12	0 0432
	360	27	0 0971
	365	1 (1)	0 0036
	370	18	0 0647
	375	5 (5)	0 0180
***Bsw*107**	175	91	0 3160
	180	9 (8)	0 0313
	185	12	0 0417
	190	66	0 2292
	195	44	0 1528
	200	23	0 0799
	205	17	0 0590
	211	16	0 0556
	216	6 (5)	0 0208
	221	2 (2)	0 0069
	227	2 (2)	0 0069
***Bbu*46**	168	12	0 0423
	170	73	0 2570
	172	17	0 0599
	174	2 (2)	0 0070
	176	41	0 1444
	182	8 (8)	0 0282
	184	72	0 2535
	186	30	0 1056
	188	29	0 1021
***Bsw*207**	228	69	0 2430
	233	100	0 3521
	238	7 (7)	0 0246
	242	35	0 1232
	244	12	0 0423
	247	34	0 1197
	252	17	0 0599
	257	10 (9)	0 0352
***Bsw*324**	317	14	0 0583
	327	2 (2)	0 0083
	329	4 (3)	0 0167
	334	8 (6)	0 0333
	338	12	0 0500
	353	10 (8)	0 0417
	365	17	0 0708
	369	23	0 0958
	374	4 (3)	0 0167
	379	22	0 0917
	384	3 (2)	0 0125
	399	12	0 0500
	401	5 (4)	0 0208
	403	35	0 1458
	408	29	0 1208
	413	20	0 0833
	416	5 (4)	0 0208
	418	8 (5)	0 0333
	421	7 (7)	0 0292

Table 6.4 Test results for pairwise Linkage Disequilibrium of 11 polymorphic loci in *Buteo ridgwayi*. Significance level of P<0.05(+). Loci that are underlined deviated significantly from HWE.

Locus	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
1		+	NS	NS	NS	+	NS	NS	NS	NS	NS
2			+	+	+	NS	+	NS	+	NS	NS
3				NS	+	+	NS	NS	+	NS	+
4					+	+	NS	+	+	NS	+
5						NS	+	+	NS	+	NS
6							+	NS	+	NS	+
7								+	+	NS	+
8									+	+	NS
9										+	+
10											NS

*Bbu*33 (1), *Bbu34* (2), *Bbu42* (3), *Bbu*51 (4), *Bsw*310 (5), *Bsw*234 (6), *Bsw*122 (7), *Bsw*107 (8), *Bbu*46 (9), *Bsw*207 (10), *Bsw*324 (11)

Table 6.5 Mean heterozygosity of other avian taxa (Ridgway's Hawk heterozygosity =0.732). Bold text refers to species with IUCN listing of either Endangered or Critical.

Species	He	No. loci	Reference
Non-raptors with similar heterozygosity			
Guira Cuckoo *Guira guira*	0.76	6	Muniz et al. 2003
White-bearded Manakin *Manacus manacus*	0.72	8	Piertney et al. 2002
Kirtland's Warbler *Dendroica kirtlandii*	0.73	23	King et al. 2005
Bicknell's Thrush *Catharus bicknelli*	0.75	6	Goetz et al. 2003
Whiskered Auklet *Aethia pygmaea*	0.72	15	Dawson et al. 2005
Blue-and-gold Macaw *Ara ararauna*	0.72	5	Caparroz et al. 2003
Raptors			
Northern Goshawk *Accipiter gentilis*	0.71	10	Topinka & May 2004
Lanyu Scops Owl *Otus elegans*	0.79	12	Hsu et al. 2003
Common Kestrel *Falco tinnunculus*	0.40	9	Nesje et al. 2000
Merlin *Falco columbarius*	0.58	7	Nesje et al. 2000
Eurasian Hobby *Falco subbuteo*	0.59	11	Nesje et al. 2000
Gyrfalcon *Falco rusticolus*	0.49	8	Nesje & Roed 2000
Golden Eagle *Aquila chrysaetos*	0.52	15	Busch et al. 2005
White-tailed Eagle *Haliaeetus albicilla*	0.59	6	Busch et al. 2005
Threatened non-raptors			
Kaka *Nestor meridionalis*	0.42	6	Sainsbury et al. 2004
Black-browed Albatross *Diomedea melanophris*	0.48	15	Burg 1999
Long-billed Black Cockatoo *Calyptorhynchus baudinii*	0.57	4	McInnes et al. 2005
Taita Thrush *Turdus helleri*	0.59	7	Galbusera et al. 2000
Mangrove Finch *Camarhynchus heliobates*	0.35	14	Petren et al. 2005
Florida Grasshopper Sparrow *Ammodramus savannarum floridanus*	0.73	6	Bulgin et al. 2003
Ijima's Leaf Warbler *Phylloscopus ijimae*	0.74	10	Saito et al. 2005
Cerulean Warbler *Dendroica cerulea*	0.77	5	Veit et al. 2005
Humboldt Penguin *Spheniscus humboldti*	0.75	7	Schlosser et al. 2003
Darwin's Finches *Geospiza spp.*	0.71-0.76	14-16	Grant et al. 2004 & Petren et al. 2005
Threatened raptors			
Lesser Kestrel *Falco naumanni*	0.70	11	Hille et al. 2003
Egyptian Vulture *Neophron percnopterus*	0.41	9	Kretzmann et al. 2003
Spanish Imperial Eagle *Aquila adalberti*	0.52	18	Martinez-Cruz et al. 2002
Madagascar Fish Eagle *Haliaeetus vociferoides*	0.30	8	Busch et al. 2005
Eastern Imperial Eagle *Aquila heliaca*	0.62	18	Busch et al. 2005
Peregrine Falcon *Falco peregrinus*	0.54	4	Brown et al. 2007

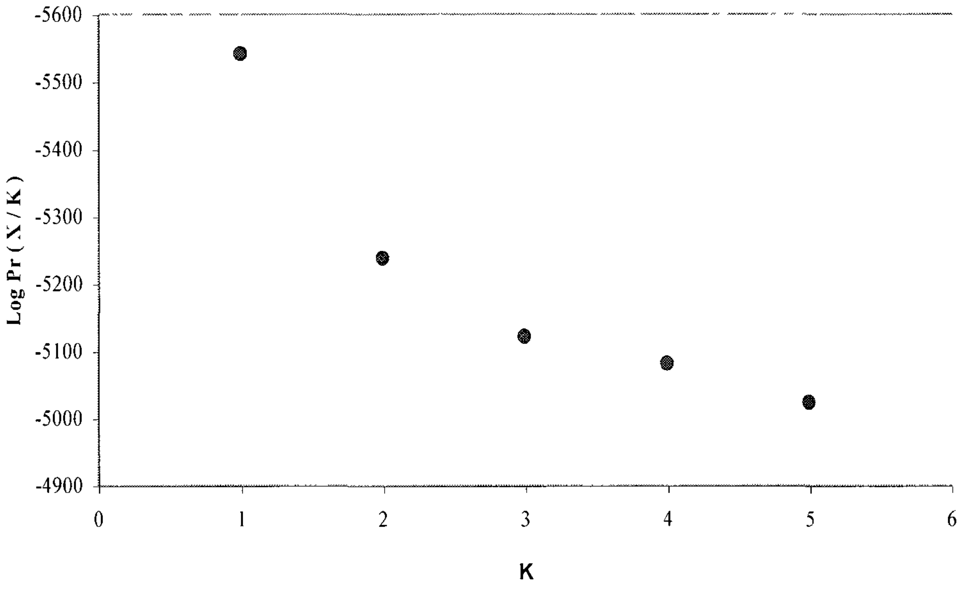

Figure 6.1 Assessment of population structure for *Buteo ridgwayi*, where Pr(X/K) is the probability for most likely number of subpopulations (K), given the genotype data (X).

Chapter 7

SOCIAL AND GENETIC MATING SYSTEM AND INBREEDING

7.1 INTRODUCTION

Molecular studies of avian breeding systems have revealed that many socially monogamous species are not genetically monogamous because paired birds commonly obtain extrapair copulations (EPCs), with extrapair offspring occurring in 70% of broods in some populations (Westneat & Sherman 1997). Griffiths et al. (2002) concluded that birds in general are rarely genetically monogamous, with extra-pair young occurring in ~90% of the species studied using molecular techniques prior to 2002. This may not be representative of all socially monogamous bird species, since the majority of EPC research has been carried out with temperate passerines (Stutchbury & Morton 2001, 2008). Investigations of mating systems of tropical taxa have been increasing (Huyvaert et al. 2000, Wallander et al. 2001, Mino et al. 2009, Krueger et al. 2008), yet there remains a need for molecular research of mating systems in nonpasserine Neotropical species (Stutchbury & Morton 2008). Of the tropical species that have been studied, most show either no or relatively low levels of extrapair paternity (Stutchbury & Morton 2001), although there have been some exceptions (Stutchbury & Morton 2008, Krueger et al. 2008).

Most *Buteo* species are socially monogamous (Ferguson-Lees & Christie 2001) but certain island populations of Galapagos Hawk *Buteo galapagoensis* are polyandrous (Mader 1978, Bollmer et al. 2003). All other *Buteo* species tend to exhibit relatively long-term pair bonds (Newton 1979). Although EPC frequencies in socially monogamous *Buteos* are not well documented, there are a few anecdotal observations in the Red-shouldered Hawk *B. lineatus* (Dykstra et al. 2008) and Swainson's Hawk *B. swainsoni* (Bechard et al. 2010). There are no publications to-date on DNA studies of socially monogamous *Buteo* species. Extra-pair young have been documented in other socially monogamous raptors including Common, American and Lesser Kestrels *Falco tinnunculus, F. sparverius* and *F. naumanni* (Korpimäki et al. 1996, Villaroel et al. 1998, Alcaide et al. 2005), and Northern Goshawk *Accipiter gentilis* (Rutz 2005). All exhibited relatively low (<12%) rates of extra pair paternity.

Within small isolated populations, the degree of genetic relatedness within the remaining population is an important factor to consider for conservation management planning. Inbreeding increases a species' risk of extinction (Frankham 1995), and if detected, may mean that translocations among isolated populations are needed. If genetic factors are not considered during population studies, extinction risks may be underestimated and unsuitable recovery strategies implemented (Frankham 2005). Molecular marker-based relatedness estimators can infer relationships among individuals with unknown ancestry, in the absence of pedigree information (Russello & Amato 2004), providing necessary information for developing appropriate management strategies.

Ridgway's Hawk is considered socially monogamous based on nest observations of three breeding pairs during one reproductive season (Wiley & Wiley 1981). Information regarding the species genetic mating system, and relatedness among the remaining individuals is unknown.

The aim of this study was to:

1. Verify the social mating system,
2. Determine the genetic mating system, and
3. Estimate genetic relatedness among adults remaining in the population, particularly breeding pairs and potential pairings.

With only a small remnant population of Ridgway's Hawk remaining and genetic evidence of inbreeding already evident (Chapter 6), the main rationale for this study was to provide ecological and genetic relatedness information to aid in the conservation management of the wild population and potential future captive populations.

7.2 METHODS

7.2.1 Field observations

Breeding pairs of *B. ridgwayi* were studied over five breeding seasons (January to July 2005-2009) within Los Haitises National Park on the northeast coast of Hispaniola (Chapter 2). Breeding pair and nest monitoring methods are detailed in Chapter 2. Number of nesting pairs observed annually from 2005 to 2009 ranged from 19 to 41 (Chapter 4).

Once a nest was located, it was visited every 1-3 days for easily accessible nests, or every 1-2 weeks for sites that were more difficult to access in terms of distance from the field site.

During each visit, breeding behaviours recorded included: nest building, food provisioning, copulations, territorial defense or displays were recorded during 3-hour observation sessions. The description of the social mating system was based on these observations. Adults were counted and, if possible, identified by band combinations during these observations. Most territories were visited more than ten times.

Hawks were banded with unique coloured aluminium identification bands, and morpho-metrics collected (Chapter 2). DNA was collected and extracted as per methods in Chapter 2. Adults were trapped using a bal-chatri noose trap and nestlings were banded on the nests when between 25 and 35 days old (Chapter 2).

7.2.2 Microsatellite genotyping

Genetic mating system, relatedness among adults in the population, relatedness between individuals in a breeding pair and potential pairings, and relatedness among nestlings in a nest were examined using 10 of the 11 polymorphic loci detailed in Chapter 6. Locus *Bsw*324 was not included in the analysis due to a high frequency of null alleles. The program CERVUS (see below) does not tolerate null alleles if the frequency is too high (Kalinowski et al. 2007). The remaining 10 loci were used for the analysis even though there was evidence of HWE and LD for several loci because CERVUS is tolerant of these types of deviations and disequilibrium. In cases of these deviations the confidence of parentage assignments should be interpreted with caution (Kalinowski et al. 2007).

7.2.3 Data Analysis

7.2.3.1 Paternity exclusion

Paternity assignment was performed using the microsatellite profiles and the likelihood-based method in the computer program CERVUS 3.0 (Kalinowski et al. 2007, 2010). To identify the putative father and to assess the statistical confidence of this identification, CERVUS calculates an LOD score (natural logarithm of the likelihood-odds ratio) for each candidate male (Kalinowski et al. 2007, 2010). A positive LOD indicates that a candidate is more likely to be the father than one randomly drawn from the population. The male with the highest score is assigned as the putative father (Kalinowski et al. 2007). The statistical confidence of this estimate is determined by measuring the difference between the LOD scores (Delta, Δ) of the males with the two highest scores (Kalinowski et al. 2007). The larger the difference, the more confidence that the male with the highest LOD score is the actual father. Critical values for Δ are generated in CERVUS by bootstrapping from the experimental population (Kalinowski et al. 2007). CERVUS takes into account genotyping errors, and limits the number of extrapair paternities according to the estimated proportion of potential fathers that have been sampled (Kalinowski et al. 2007).

Parameters used in CERVUS for maximum likelihood paternity assignment included 100,000 simulation cycles with relaxed and strict confidence levels set at 80% and 95%, respectively. The proportion of candidate parents sampled was 0.20. The proportion of loci typed and loci mistyped were 0.90 and 0.01, respectively. The minimum number of typed loci used for the analysis was seven.

7.2.3.2 Relatedness

Relatedness among the sampled adults of the population, between breeding pairs, between potential pairings, and among broods was carried out using the genetic software program KINGROUP v2 (Konovalov et al. 2004). Relatedness estimators using co-dominant markers are unbiased even when allele frequencies are estimated from relatively small samples (Queller & Goodnight (1989), making them the best available markers for estimating relatedness in wildlife species (Blouin 2003, Blouin et al. 1996, DeWoody 2005). They have been shown to be a valuable tool for inferring relationships among individuals with unknown ancestry, in the absence of pedigree information (Russello & Amato 2004).

Relatedness was determined by three methods: pairwise relatedness coefficients (r), pedigree relationships, and kinship reconstruction. Pairwise relatedness coefficients and pedigree relationships were used to detect relationships between significantly related individuals including that of parent-offspring, full siblings and half-siblings. Kinship reconstruction was used to detect more distant genetic relationships, similar to that of distant cousins by grouping related kin. These methods were chosen for their proven accuracy in estimating relatedness among individuals and groups in a population (Gautschi et al. 2003).

Pairwise relatedness coefficients were calculated based on Queller & Goodnight (1989). This relatedness estimator ranges from -1 to +1. A positive value indicates that two individuals share more alleles by descent than expected by chance. First order relatives such as parent-offspring or full siblings should have an ‘r’ value of approximately 0.5, and half-siblings an ‘r’ of 0.25. Unrelated individuals should have an ‘r’ value close to or less than 0. Pairwise relatedness coefficients among all adults and within broods were compared to theoretical values using t-tests. A genetic relationship between two individuals was considered significant ($p<0.05$) by KINGROUP (Konovalov et al. 2004), if the pairwise relatedness coefficient was ≥ 0.25, similar to that of half-sibling relatedness or greater.

Pedigree relationships were tested to determine the likelihood that a dyad (two individuals) shared a hypothesized pedigree relationship (the primary hypothesis), and whether the hypothesized relationship was significantly more likely than the alternative relationship (the null hypothesis). The primary hypothesis was that individuals of a dyad were parent-offspring or full siblings. The null hypothesis was that individuals of a dyad were unrelated. Type II error was reported as the percent of false rejections of the primary hypothesis at a significance level of $p<0.05$.

In KINGROUP, Full Sibling Reconstruction (FSR) Algorithms were created using a Simpson-assisted Descending Ratio (SDR) to reconstruct groups of kin by evaluating alternative partitions of the genotype dataset according to an overall likelihood (Konovalov et al. 2004). The SDR method is the most accurate for smaller number of loci (>6), and the most robust to genotyping errors and the presence of unrelated individuals (Konovalov 2006). The primary hypothesis tested was that individuals of a dyad were at least as related as first cousins ($r=0.125$) and belonged in the same subgroup. The null hypothesis was that individuals of dyad were not related and should be split in to different subgroups. This analysis tested for more distant genetic relationships that existed, but not considered 'statistically' significant.

7.3 RESULTS

7.3.1 Social mating system and copulation behaviour

During all observations, no more than two adults were ever observed interacting non-aggressively within a territory. Aggressive interactions between adjacent individuals or pairs were observed during aerial territorial displays.

Whenever individual birds were identified from band combinations, identification confirmed the attending female and male at nests to be the adults paired within the territory. No non-paired males were observed provisioning food or even seen near the resident female in an active territory. However, with a limited ability to identify individuals during encounters, this does not preclude the possibility of extra-pair copulations. However it does suggest that EPCs are not a common occurrence.

Copulations were observed during all stages of the breeding episode (Appendix 7.1). Copulations were recorded during nestbuilding (47 observations), incubation (5), nestling (7) and early fledgling stages (1), and were recorded during all months from November through June. Peaks in copulation frequencies occurred just prior to egg-laying (January-March) or just after a nest had failed (April-May).

Copulations were also recorded in late November (1 observation) and December (2), although these were general observations made by field researchers that were not part of regular territory watches. The observations in late December were accompanied by early nestbuilding behaviour. It was also observed that pairs generally spent much of their time together in the nest valley during November and December (T. Hernandez and H. Pollanca pers comm.). This is consistent with the belief of Wiley & Wiley (1981), based on observations of territorial flights in October, that Ridgway's Hawk maintain year-round territories.

Copulation behaviour between two individuals may be indicative of whether copulations are within pair or extrapair. Female solicitation followed by male mounting without interruption by the female could be suggestive of a within pair copulation. Of 62 observed copulation attempts, 60 were carried out without any interruption by the female. On two occasions, a male mounted the female but the female did not lift her tail to allow the copulation to continue. In both instances the male dismounted and remained perched next to the female and was identified as the attending male. A typical copulation consisted of a male landing next to a female at a preferred perch near the nesting tree. These preferred perches were generally but not always conspicuous lone trees above the canopy but were nearly always within 100m of the nest tree. Copulations did occur on the nests themselves, although this was not common. One copulation occurred on a stump on the ground within 6m of the nest tree. After landing the male would then hop on to the back of the female. The female remained flat and horizontal with her head down while the male flapped his wings to keep his balance. Vent contact was made by the female's tail being pushed to the side by the male. Copulations were accompanied throughout the entire sequence by high pitched squeaking calls (see Wiley and Wiley 1981 for vocalization details), similar to those heard during food passes. Copulations were not necessarily preceded by food passes. The copulation duration ranged from 6 to 30 seconds. One pair in 2008 was observed copulating on February 26, March 6, 7 and 10th, with copulation frequencies of 3 copulations per 4 hour observation period during the period leading up to egg-laying.

All observations of courtship, territorial displays, nesting and breeding behaviour of Ridgway's Hawk confirmed a monogamous social mating system for the species. No verified extra-pair copulations were observed in the study period. However, since not all individuals could be positively identified during all copulations this does not preclude the possibility of EPCs in this species.

7.3.2 Microsatellite genotyping

One hundred and twelve nestlings from 54 broods, and 34 adults were genotyped. Eighty-three different alleles were found from 10 loci, with an observed heterozygosity of 0.766 ± 0.106 (Table 7.1, more detail in Chapter 5). The mean polymorphic information content of all loci was 0.718 ± 0.134 (Table 7.1). The combined probability of non-exclusion for the marker set was 0.001 (Table 7.1).

7.3.3 Genetic mating system: paternity assignment

7.3.3.1 Paternity assignment

The attending male was assigned as the putative father for 29 out of 30 nestlings from 19 broods (Appendix 7.2). From 2005-2007, none of the broods showed evidence of extra pair young but in 2008, there was one instance of an attending male not being assigned as the actual father to 1 of the 2 nestlings. A male in a territory >3 km away (#6042) was assigned as the putative father to one nestling (#8012) but the confidence level of the assignment was not significant since there was little to no difference in the LOD scores between the two males (Delta value of 0). Both these males had similar genotypes, and both males mismatched with the nestling at just one locus. Further inspection of the relationship between these males found that the assigned non-attending male #6042 was significantly related to attending social male #7004 (relatedness coefficient 'r' = 0.52, p<0.00) and was likely either a parent-offspring or full sibling relationship. Thus it is possible this one case was not an instance of an extra-pair fertilization.

7.3.4 Relatedness

7.3.4.1 Brood relatedness

Brood relatedness values were helpful in determining potential EPP in cases where one or both parents were not genotyped. The relatedness coefficient among nestlings in the 40 broods sampled over the study period ranged from 0.32 to 0.62 and averaged 0.48 ± 0.08 (Appendix 7.2). These values did not significantly differ from the expected 0.5 ($t_{1,39}$=-0.35, p=0.73) and indicated full-sibling relatedness on average for all broods. For comparison, relatedness coefficients were obtained from known half-siblings (based on social pairings); nestlings from nests of different years where one parent was identified from the previous year and the other parent was a new mate. Half-sibling relatedness coefficients ranged from 0.16 to 0.29 and averaged 0.23 ±0.04 (n=12). Relatedness coefficients of half-siblings did not differ significantly from the expected 0.25 ($t_{1,11}$=-1.58, p=0.09) and were significantly lower compared to relatedness coefficients of nestlings within the same brood ($F_{1,51}$=-11.12, p<0.00). This suggests that all 40 broods sampled over the study period consisted of full siblings with no cases of extrapair young.

7.3.4.2 Adult relatedness

The pairwise relatedness coefficients among all adults sampled ranged from -0.54 to 0.63, and averaged -0.03 ± 0.18 (n=561). The average adult relatedness did not differ significantly from zero ($t_{1,560}$ = -1.62, p=0.11) indicating that the adults sampled in this study were not, on average, significantly related to each other. Based on a pedigree analysis with 10,000 simulations, 6.1% of the adult pairwise comparisons were between 1^{st} order relatives (parent-offspring or full-sibling), and 93.9% of pairwise comparisons were either unrelated adults or there was not sufficient evidence to support close relatedness at the p=0.05 significance level. Type II error rate reported (rate of false rejection of the primary hypothesis) was 4.7%.

To determine if any patterns of genetic relatedness existed within either gender, relatedness coefficients were also compared among the adult females sampled and among the adult males sampled. Relatedness among the adult females was found to be significantly higher than relatedness among the adult males ($t_{1,279}$ = -2.54, p=0.01).

Relatedness among the 20 adult females ranged from -0.46 to 0.45 and averaged 0.09 ± 0.17. The average relatedness value was significantly different from zero ($t_{1,189}$ =1.06, p=0.03) indicating that the adult females sampled in this study were, on average, somewhat related to each other. A test of pedigree relationships using 10,000 simulations, found that 18.7% of pairwise comparisons were between 1st order related females, and the remaining 81.3% were either unrelated females or there was not sufficient evidence to support close relatedness at the p=<0.05 significance level. Type II error rate reported was 5.1%.

Relatedness among the 14 adult males sampled ranged from -0.59 to 0.52 and averaged -0.08 ± 0.16. The average relatedness value was significantly different from zero ($t_{1,90}$ = -4.16, p<0.00). However the significance was negative indicating that on average, adult males sampled in this study were significantly unrelated to each other (negative relatedness coefficients). A test of pedigree relationships using 10,000 simulations found 3.3% of pairwise comparisons were between 1st order related males and the remaining 96.7% were either unrelated males or there was not sufficient evidence to support relatedness at the p<0.05 significance level. Type II error reported was 7.1%.

7.3.4.3 Relatedness between known pairs and potential pairings (Female-Male dyads)

Relatedness coefficients of the eight sampled breeding pairs ranged from -0.07 to 0.55 and averaged 0.14 ± 0.22 (Appendix 7.2). Four out of the eight breeding pairs exhibited pairwise relatedness values greater than 0. One pair was significantly related (p<0.00), with a relatedness coefficient of 0.56 indicating either a full-sibling or parent-offspring relationship. A second pair was also related (p=0.06) with a relatedness coefficient of 0.21 indicating a potential half-sibling relationship. The remaining two pairs had relatedness coefficients of 0.12 and 0.14, although the relatedness values were not statistically significant (p=0.12 and p=0.18). Kinship reconstruction placed both these breeding pairs (pair #5005 x #5006 and pair #5027 x #5028) within the same kin subgroups (Table 7.2) suggesting that these pairings were related at an order similar to that of first cousins.

Relatedness coefficients of potential breeding pairs (Female-Male dyads) ranged from -0.45 to 0.62 and averaged -0.03 ± 0.18 (n=272). This average relatedness was not significantly different from zero ($t_{1,\,278}$ = -1.45, p= 0.17) indicating that, on average, matings among the sampled adults would not be between closely related individuals. However, still a fairly high percent of the potential random pairings among the 20 females and 14 males sampled (18.1%, 49/272) would be dyads with relatedness values similar to or greater than that of half-siblings (r >0.20).

Kinship reconstruction found that the 34 sampled adults consisted of 10 kin subgroups, with only three adults placed in lone groups and not related to the others (Table 7.2). All other adults were grouped with at least one other adult that was as related as a first cousin. The largest subgrouping contained six related adults. There did not appear to be any obvious pattern toward either sex or area in any of the kin subgroups (Table 7.2). The individual sampled at Llenada Grande (#6044) was from the eastern side of Los Haitises National Park, yet was placed in the same subgroup with other adults from the main study area on the western side of the Park, rather than within a lone subgroup. This represents a distance of 22.3 km between Llenada Grande and the nearest neighbour within that subgroup.

7.4 DISCUSSION

7.4.1 Social mating system

Nest site and territory observations verified a socially monogamous mating system for Ridgway's Hawk, as originally proposed by Wiley & Wiley (1981). This is the most common social mating system of both temperate and tropical *Buteo*s (Ferguson-Lees & Christie 2001). The one exception being the Galapagos Hawk which consists of several island subpopulations that ranges from social monogamy to polyandry (Bollmer et al. 2003). All other *Buteos* tend to exhibit relatively long-term pair bonds (Newton 1979). However, there are single records of three adults tending nests for *B. swainsoni* (Cash 1989), Red-tailed Hawk *B. jamaicensis* (Santana et al. 1986), and Common Buzzard *B. buteo* (Barrientos & López-Darias 2006), although the sexes and the exact roles of the attending adults were not known. For the present study, there were no observations of more than two adult Ridgway's Hawks at any nest during the five-year period. The closest taxonomic relative to Ridgway's Hawk is the Red-shouldered Hawk *B. lineatus*. There is a single record of three adult Red-shouldered Hawks (two males and one female) attending a nest in Florida (Dykstra et al. 2008). The Puerto Rican Broad-winged Hawk *B. platypterus brunnescens* is the geographically closest forest dwelling *Buteo* to Ridgway's Hawk. There is one reported incident of a nesting female accepting food provision from an intruding male in the absence of the attending male, with no attempt by either bird to copulate (Delannoy & Cruz 1988).

Within avian taxa, socially monogamous males appear to have evolved two strategies to ensure paternity: mate guarding (Birkhead 1979) and/or frequent within-pair copulations (Birkhead et al. 1987). Ridgway's Hawks seem to have employed the latter strategy. During the study period, copulations were observed between breeding pairs during all stages of the breeding episode, and were frequent during late nestbuilding and early incubation stages. Males were often away from their nests for extended periods of time to hunt and provide food to the female, and hence could not effectively guard their mates.

Extra-pair copulations (EPCs), or even attempts by non-attending males to obtain EPCs were not observed during the 5-year study which would call into question the *sperm competition hypothesis* (Moller & Birkhead 1992) for Ridgway's Hawk. Males would not need to constantly dilute sperm from potential male intruders if EPCs were very infrequent. Ridgway's Hawk behaviour during field observations most strongly supports the *pair-bonding hypothesis* (Newton 1979). Copulations were observed throughout the breeding season. Pairs were observed copulating during incubation, early and late nestling stages, and post-fledging.

7.4.2. Genetic Mating System

The results from the present study indicate that the genetic mating system of Ridgway's Hawk is monogamous as extra-pair fertilizations occur rarely, if at all. The paternity analysis did not document any extra-pair young within the sampled nests and for all broods relatedness between sib-mates did not differ from the expected 0.5. One instance of a non-attending male being assigned as the putative father to one of two nestlings was not significant in confidence, and the close relatedness between the two candidate fathers made the assignment inconclusive.

To date there have been no published studies of genetic mating systems for a socially monogamous *Buteo*. There are a few anecdotal EPC observations for several species including *B. lineatus* (Dykstra et al. 2008) and *B. swainsoni* (Bechard et al. 2010), but no confirmed extra-pair young. Since EPCs can predict EPP (Townsend 2009), it is possible that a very low rate of EPP does occur in other *Buteos*. However, as in Ridgway's Hawk, these rates would likely be so low as to be considered effectively genetically monogamous. As an example, in all the literature published on *Buteos* over the last half century, there have only been a handful of EPC records (see Dykstra et al. 2008, Bechard et al. 2010).

Extra-pair young have been reported in other similar sized socially monogamous raptor species including the Eurasian Kestrel (1.9% in Korpimäki et al. 1996), the Lesser Kestrel (3.8 - 9.6% in Alcaide et al. 2005) and the Northern Goshawk (9.4% in Gavin et al. 1998). The highest rate of EPP for a similar sized hawk was found in the American Kestrel at 11.2% (Villaroel et al. 1998).

The findings of the present study are consistent with investigations of island species and of tropical bird populations, both of which tend to exhibit low rates of EPP (Griffiths 2000, Stutchbury & Morton 2001). Griffith (2000) found lower rates of EPP for species on islands compared to mainland counterparts. The authors mention several nonmutually exclusive hypothesis to explain lower EP rates on islands including: reduced genetic variability in island species, reduced breeding densities, lower food abundance, phenotypic plasticity to harsher island environments, and the cost of mate abandonment on islands (where mates are less numerous).

Stutchbury & Morton (1995) proposed the *breeding synchrony hypothesis* to explain low rates of EPP in the tropics. This hypothesis states that the shorter breeding season in temperate zones promotes highly synchronized breeding and a high availability of fertile females at the same time (up to 72%) resulting in increased EPCs. In the tropics most species breed asynchronously, thus fewer females are fertile at the same time (as few as 8%) during a longer breeding period resulting in significantly fewer EPCs . During the present study, Ridgway's Hawks were observed breeding over a seven-month period with a large temporal variation in egg-laying. Although most pairs laid during a 3 month period from mid-January to mid April, some pairs laid eggs as late as July (Chapter 4).

The genetic mating system of Ridgway's Hawk also corresponds with the male parental care hypothesis (reviewed in Neudorf 2004). Male Ridgway's were observed incubating and were the main food provider to the nestlings, and therefore would have reduced time to pursue EPCs.

The challenge in applying hypotheses to a given taxon is that often certain life history traits co-occur (Westneat & Stewart 2003) and it is difficult to determine to what extent each trait may contribute to EPP rates. For example, longevity and male parental care are both life-history traits for several taxa including seabirds (Arnold & Owens 2002), owls (Arsenault et al. 2002, Saladin et al. 2007), parrots (Masello et al. 2002), and vultures (Decker et al.

1993). This phylogenetic component to variation in EPPs also adds to the challenge of trying to explain or predict EPP rates. As a general rule, EPP rates tend to be higher in passerines and lower in raptors and seabirds (Westneat & Sherman 1997). However recent studies have reported species which appear to be ‘exceptions to the rule’. Genetic monogamy or very low EPP rates have been reported in several passerines (Kleven et al. 2008, Taylor et al. 2008, Maguire & Mulder 2008), and high levels of EPP have been found in albatross (Huyvaert et al. 2000). At the same time, recent studies are also reporting many species conforming to the original ‘rules’ of EPP rates, including low to no EPP in raptors (Ridgway’s Hawk in this study, Arsenault et al. 2002, Saladin et al. 2007, Hogan & Cooke 2010), seabirds (Wojczulanis-Jakubas et al. 2009, Anker-Nilssen et al. 2008, 2010) and higher EPP in temperate passerines (Stewart et al. 2010). It is not surprising that factors contributing to the frequency of EP mating are challenging to resolve since just a few ecological or biological differences between populations of closely related species can result in very large variation in EPP (Kingma et al. 2009).

7.4.3 Relatedness

7.4.3.1 Adults

On average, adult Ridgway’s Hawks were not significantly related to each other; meaning not related at a level similar to that of half-sibling or greater. However, the analysis revealed that the 34 sampled adults formed only 10 kin groups, and that many (85%) of adults were related to several others at a level similar to that of first cousins. This may become a potential problem in the near future if the population continues to decrease. Fortunately, it appears that individuals within the same kin subgroups are distributed throughout Los

Haitises and are not nesting adjacent to one another. Although this may help prevent close inbreeding between parent-offspring, it may also be indicative of the difficulties in finding a territory near the natal site.

Adult males were not significantly related to each other. However, adult females were significantly related to each other on average. This may be a result of a potential female biased nestling sex-ratio observed within the population (Chapter 8). Breeding pairs appear to be producing more females annually, with many nests fledging two females (Chapter 8).

7.4.3.2 Known and potential pairings

Genetic analyses revealed that inbreeding does occur within the population of Ridgway's Hawk. Close inbreeding occurs when parent-offspring or full-sibling pairs are formed (Rowley et al. 1993). Although close inbreeding has been recorded in wild populations of American Kestrel (*Falco sparverius*; Bowman et al. 1987 cited in Stewart et al. 2007), Merlin (*F. columbarius*; James et al. 1987), Peregrine Falcon (*F. peregrinus*; Tordoff & Redig 1999), Osprey (*Pandion haliaetus*; Postupalsky 1989) and Cooper's Hawk (*Accipiter cooperii*; Rosenfield & Bielefeldt 1992, Stewart et al. 2007) these reports are rare and represent single occurrences.

Two of the eight breeding pairs were between significantly related individuals, and two more pairs were related similar to that of first cousins. In addition, the analysis of potential random pairings among the 34 adults sampled indicated that *c.*18% of pairings would be between related individuals, which is higher than that found for large, widely distributed populations. Blomqvist et al. (2010) found strong evidence of inbreeding depression in the form of reduced hatching success and increased embryonic mortality, in a population of endangered shorebird *Calidris alpina schinzii* with a 9 -13% inbreeding rate.

Inbreeding is almost unavoidable in the small isolated populations typical of endangered species (Frankham et al. 2002) and may be a contributing factor to population extinction in small populations (Frankham 2005). There is a significantly higher extinction risk of inbred lines when compared to outbred lines in controlled laboratory experiments (Frankham 1995; Bijlsma et al. 2000; Reed et al. 2002, 2003, Wright et al. 2008). These studies indicate an increased extinction risk with not only full-sib inbreeding but also with lower orders of inbreeding. Inbreeding can increase extinction risk through selection of deleterious recessive alleles and/or by decreasing average fitness and gene diversity (Hedrick 1994, Wright et al. 2008).

Island populations, particularly those of insular endemic species, have elevated inbreeding coefficients (as was found for Ridgway's hawk, Chapter 6) and are therefore likely to experience increased levels of inbreeding depression (Frankham 1998). This can act in conjunction with demographic stochasticity and environmental stresses to greatly increase the likelihood of extinction (Frankham 1998, Bijlsma et al. 2000).

7.4.4 Conclusions

The monogamous social and genetic mating systems of Ridgway's Hawk are consistent with the general predicted mating systems for a tropical island endemic raptor. Knowledge of the mating systems, and relatedness within the remaining individuals, can be used to improve the efficacy of conservation management using planning tools, such as calculations of minimum viable population size and PHVAs. If the mating system is known, field observations of breeding pairs can be used to accurately construct pedigrees. Similarly, the estimates of relatedness from this current study can be used to estimate the relatedness of new pairings, and provide a baseline measure of potential levels of inbreeding.

The results of the analysis of breeding pair relatedness provide cause for concern. Evidence of inbreeding was found in four of the eight sampled breeding pairs, representing a tangible threat to the species. Eighteen percent of possible random pairings (female-male dyads) from the 34 sampled adults would also be between related individuals. If this sample is representative of the entire population and >18% of the remaining breeding pairs are related, there could be serious implications for the future survival of the species, particularly if the species continues to decline in population size and range due to other direct threats such as habitat loss and persecution.

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Table 7.1 Characteristics of microsatellite loci used for paternity assignment and estimating relatedness of Ridgway's Hawk.

Locus	**Alleles**	**n[a]**	**He[b]**	**PIC[c]**	**Pexclusion [d]**
*Bbu*33	4	142	0.538	0.432	0.855
*Bbu*34	4	135	0.617	0.544	0.802
*Bbu*42	8	147	0.799	0.769	0.572
*Bbu*46	9	142	0.823	0.799	0.521
*Bbu*51	6	136	0.755	0.718	0.638
*Bsw*107	11	144	0.809	0.783	0.543
*Bsw*122	12	139	0.828	0.812	0.493
*Bsw*207	8	142	0.783	0.747	0.598
*Bsw*234	8	138	0.820	0.794	0.533
*Bsw*310	13	142	0.883	0.869	0.786
Total	83	-	-	-	0.0001*
Mean	8.3	-	0.766	0.718	-
SD	3.1	-	0.106	0.134	-

[a] Number of individuals typed including adults and nestlings, [b] Expected Heterozygosity, [c] Polymorphic Information Content, [d] Probability of exclusion, *Total probability of exclusion using all loci, from Marshall et al. (1998).

Table 7.2 Results of FSR Algorithm analysis for relatedness of sampled Ridgway's Hawk adults. Pairings in the same subgroup are presented in bold text.

Adult ID	Area	Sex	Kin Subgroup
#5001	Antonitos-Antonito	F	1
#5004	Biernan-Jose Pirula	F	2
#5009	Cacata-Pedro	F	3
#5005	**Britos-Renardo**	**F**	**4**
#5006	**Britos-Renardo**	**M**	**4**
#6053	Tiladora-Medrano	F	4
#7028	Guallullos-Gonzales	F	4
#7034	Caimonis-Tison Haytiano	F	4
#6039	Congo-Modesta	F	5
#7039	Mata Limon-Francisco Siriaco	F	5
#6004	Aguatico-Siriaco	M	5
#6011	Arrollitos-Santo Maito	M	6
#7029	Cacatona-Jesus	F	6
#6003	Aguatico-Siriaco	F	7
#7004	Aguatico-Sariano	M	7
#7036	Congo-Modesta	F	7
#7037	Aguatico-Pin	M	7
#8043	**Llalla-Beato**	**F**	**7**
#6042	**Llalla-Beato**	**M**	**7**
#6041	**Indios-Munal**	**F**	**8**
#7035	**Indios-Munal**	**M**	**8**
#5022	Cotorra-Bigote	M	8
#7030	Aguatico-Juan Mojao	M	8
#5017	Casa Grande-Carlos	M	9
#6002	Aguatico-Esdito	F	9
#6044	Llenada Grande	F	9
#7031	Aguatico-Juan Mojao	F	9
#7033	Mata Limon-Nalsiso	M	9
#5027	**Malena-Moncholo**	**F**	**10**
#5028	**Malena-Moncholo**	**M**	**10**
#6030	Caimonis-Balon	M	10
#6035	Posito-Nolo	F	10
#7038	Aguatico-Santico	M	10
#5016	Casa Grande-Carlos	F	10

APPENDIX 7.1 Number of copulations recorded by month and breeding stage in Ridgway's Hawk from 2005-2009.

	January	**February**	**March**	**April**	**May**	**June**
Nest building [a]	15	22	9	1	0	0
Incubation	0	2 [b]	2	1	0	0
Young nestling	0	0	1 [c]	0	0	0
Old nestling	0	0	0	3	2	1
Fledgling	0	0	0	0	1	0
Recently failed nest	0	0	1 [d]	7 [e]	7 [f]	0

[a] First nest attempts.
[b] One of these was a copulation after the first egg of a two egg laid clutch had been laid.
[c] Nest with 6 day old nestlings.
[d] Failed during incubation.
[e] Three of these failed with young chicks, others failed at unknown stage.
[f] Five of these failed with nestlings, two were 2nd nest attempts that failed with eggs.

APPENDIX 7.2 Results of CERVUS paternity assignment and KINGROUP breeding pair and nestling relatedness coefficients for sampled Ridgway's Hawks from 2005 to 2008.

Year	Territory	AF / AM ID	Pair r [a], P-value	Nestling ID	No. of loci mismatch with AF	No. of loci mismatch with AM	LOD score confidence [b]	Assigned male	Brood r [c], P-value
2005	Britos-Renardo	5005 / 5006	0.092, p=0.217	5007	0 / 10	0 / 10	5.90E+00, **	5006	0.46, p=0.005
				5008	0 / 10	0 / 10	3.00E+00, *	5006	
2005	Cacata	5009 / NS	-	5010	0 / 9	-	-	-	0.65, p=0.000
				5011	0 / 9	-	-	-	
2005	Indios-Munal	6041 / 7035	0.212, p=0.063	5013	0 / 10	0 / 10	7.65E-01, *	7035	-
2005	Casa Grande-Carlos	5016 / 5017	-0.047, p=0.501	5018	0 / 9	0 / 10	2.87E+00, *	5017	0.50, p=0.003
				5019	0 / 9	1 / 10[d]	3.98E-01, *	5017	0.39, p=0.022
				5020	0 / 9	0 / 10	3.23E+00, **	5017	0.48, p=0.005
2005	Cotorra-Bigote	NS / 5022	-	5023	-	0 / 10	9.22E+00, **	5022	0.57, p=0.001
				5024	-	0 / 10	7.37E+00, **	5022	
2005	Malena-Moncholo	5027 / 5028	0.143, p=0.115	5029	0/9	0 / 7	5.78E+00, **	5028	-
2005	Mata Limon-Lico	NS / NS	-	5032	-	-	-	-	0.53, p=0.002
				5033	-	-	-	-	
2006	Arrollitos-Santo Maito	NS / 6011	-	6012	-	0 / 9	3.10E+00, **	6011	0.41, p=0.013
				6013	-	1 / 10[d]	1.83E+00, *	6011	
2006	Britos-Neybi	NS / NS	-	6019	-	-	-	-	0.33, p=0.010
				6020	-	-	-	-	
2006	Cacata-Pedro	NS+ / NS-		6025	-	-	-	-	0.48, p=0.001
				6026	-	-	-	-	

APPENDIX 7.2 CONTINUED

Year	Territory	AF / AM ID	Pair r [a], P-value	Nestling ID	No. of loci mismatch with AF	No. of loci mismatch with AM	LOD score confidence [b]	Assigned male	Brood r [c], P-value
2006	Cacata-Ramon	NS / NS -	-	6027	-	-	-	-	0 39, p=0 016
				6028	-	-	-	-	
2006	Carmonis-Balon	NS / 6030	-	6031	-	0 / 10	4 90E+00, **	6030	0 49, p=0 010
				6032	-	0 / 10	5 65E+00, **	6030	
2006	Casa Grande-Juan	NS / NS -	-	6033	-	-	-	-	0 51, p=0 001
				6034	-	-	-	-	
2006	Malena-Moncholo	5027 / 5028	0 143, p=0 115	6045	0 / 9	0 / 7	3 95E+00, **	5028	0 54, p=0 000
				6046	0 / 10	0 / 7	5 65E+00, **	5028	
2006	Mata Limon-Lico	NS / NS -	-	6048	-	-	-	-	0 48, p=0 001
				6049	-	-	-	-	
2006	Mata Limon-Pilar	NS / NS -	-	6050	-	-	-	-	0 45, p=0 001
				6051	-	-	-	-	
2006	Tiladora-Medrano	6053 / NS	-	6054	1 / 10[d]	-	-	-	0 38, p=0 002
				6055	0 / 9	-	-	-	
2007	Aguatico-Jose	NS / NS	-	7001	-	-	-	-	0 48, p=0 001
				7002	-	-	-	-	
2007	Aguatico-Sariano	NS / 7004	-	7005	0 / 10	0 / 10	1 03E+01, *	7004	0 55, p=0 000
				7006	0 / 10	0 / 10	6 67E+00, *	7004	
2007	Casa Grande-Carlos	NS+ / 5017	-	7008	-	0 / 10	5 76E+00, **	5017	-

APPENDIX 7.2 CONTINUED

Year	Territory	AF / AM ID	Pair r [a], P-value	Nestling ID	No. of loci mismatch with AF	No. of loci mismatch with AM	LOD score confidence [b]	Assigned male	Brood r [c], P-value
2007	Calle Sol-Plinio	6039 / NS	-	7009	1 / 10[d]	-	-	-	0.40, p=0.010
				7010	0 / 9	-	-		-
2007	Cacata-Julito	NS / NS	-	7011	-	-	-	-	0.51, p=0.001
				7012	-	-	-		-
2007	Cacata-Ramon	NS / NS	-	7013	-	-	-	-	0.62, p=0.000
				7014	-	-	-		-
2007	Cacata-Pedro	7029 / NS	-	7015	0 / 9	-	-	-	0.64, p=0.001
				7016	0 / 9	-	-		-
2007	Arrollitos-Sila	NS / NS	-	7017	-	-	-	-	0.47, p=0.001
				7018	-	-	-		-
2007	Indios-Munal	6041 / 7035	0.212 p= 0.63	7021	0 / 10	0 / 10	3.86E+00, *	7035	-
2007	Tiladora-Medrano	6053 / NS	-	7022	0 / 10	-	-	-	0.61, p=0.000
				7023	0 / 9	-	-		-
2007	Britos-Renardo	NS+ / 5006	-	7024	-	0 / 10	5.90E+00, **	5006	0.48, p=0.005
				7025	-	0 / 10	3.00E+00, *	5006	
2007	Britos-Neybi	NS / NS	-	7026	-	-	-	-	0.32, p=0.030
				7027	-	-	-	-	
2007	Casa Grande-Carlos 2	NS+ / 5017	-	7040	-	0 / 10	2.31E+00, *	5017	-
2008	Guallullos-Gonzales	7028 / NS	-	8001	0 / 9	-	-	-	0.45, p=0.001
				8002	0 / 10	-	-	-	

APPENDIX 7.2 CONTINUED

Year	Territory	AF / AM ID	Pair r [a], P-value	Nestling ID	No. of loci mismatch with AF	No. of loci mismatch with AM	LOD score confidence [b]	Assigned male	Brood r [c], P-value
2008	Llalla-Beato	8043 / 6042	0 555, p= 0 000	8003	0 / 8	0 / 10	6 86E+00, **	6042	0 55, p=0 000
				8004	0 / 8	0 / 10	6 65E+00, **	6042	
2008	Cacata-Pedro	7029 / NS	-	8005	0 / 9	-	-	-	0 63, p=0 000
				8006	0 / 9	-	-	-	
2008	DeVio-Jose	NS / NS	-	8008	-	-	-	-	0 43, p=0 003
				8009	-	-	-	-	
2008	Arrollitos-Juan	NS / NS	-	8010	-	-	-	-	0 56 p=0 000
				8011	-	-	-	-	
2008	**Aguatico-Sariano**	**NS / 7004**	**-**	**8012**	-	**1 / 10**	**1.67E+01, ns**	**6042**	0 62, p=0 000
				8013	-	**0 / 10**	**9.41E+00, ****	**7004**	
2008	Caimonis-Balon	NS / 6030	-	8014	-	0 / 9	5 80E+00, **	6030	0 46, p=0 005
				8015	-	1 / 9[d]	1 67E+00, *	6030	
2008	Mata Limon-Nolo	NS / 7033	-	8016	-	0 / 10	7 18E+00, **	7033	-
2008	Britos-Ramon	NS / NS	-	8019	-	-	-	-	0 43, p=0 005
				8020	-	-	-	-	
2008	Tiladora-Medrano	6053 / NS	-	8021	1 / 10	-	-	-	0 56, p=0 000
				8022	0 / 10	-	-	-	
2008	Arrollitos-Jeron	NS / NS	-	8025	-	-	-	-	0 54, p=0 000
				8026	-	-	-	-	
2008	Arrollitos-Lico	NS / NS	-	8027	-	-	-	-	0 47, p=0 001
				8028	-	-	-	-	

APPENDIX 7.2 CONTINUED

Year	Territory	AF / AM ID	Pair r [a], P-value	Nestling ID	No. of loci mismatch with AF	No. of loci mismatch with AM	LOD score confidence [b]	Assigned male	Brood r [c], P-value
2008	Arrollitos-Santo Maito	NS / 6011	-	8029	-	1 / 10[d]	1.91E+00, *	6011	0.39, p=0.063
				8030	-	0 / 10	5.88E+00, **	6011	
2008	Arrollitos-Sila	NS / NS	-	8031	-	-	-	-	0.61, p=0.000
				8032	-	-	-	-	
2008	Calle Sol-Plinio	NS+ / NS-		8037	-	-	-	-	0.49, p=0.001
				8038	-	-	-	-	
2008	Mata Limon-Lico	NS / 7033	-	8044	-	1 / 10[d]	3.00E+00, *	7033	-

AF Attending female, AM Attending male, ID identification number, NS Not sampled

+ New mate

[a] Breeding pair relatedness coefficient and p-value

[b] parental assignment confidence where ** is strict confidence (95%) and * is relaxed confidence (80%), ns is non-significant (no confidence)

[c] Brood relatedness coefficient and p-value

[d] mismatched loci likely due to genotyping error

Chapter 8

REVERSED SEXUAL SIZE DIMORPHISM AND NESTLING SEX-RATIOS

8.1 INTRODUCTION

Females are either smaller or similar in size to males for the majority of bird species. However, most diurnal raptors exhibit reversed sexual size dimorphism (RSD) and females are larger than males (Snyder & Wiley 1976, Ferguson-Lees & Christie 2001). An expansive literature has accumulated to explain RSD in birds, but as yet there is little consensus (see reviews in Andersson & Norberg 1981, Ydenberg & Forbes 1991, Bildstein 1992).

Research on raptors, predominantly species exhibiting RSD, have shown that significant biases in the sex-ratio of nestlings can depend on demographic factors and environmental conditions experienced by the parents during the breeding episode (Korpimaki et al. 2000, Byholm et al. 2002, Hipkiss et al. 2002, Magrath et al. 2007). Biases can potentially occur due to different energy requirements between male and female chicks, or in response to adverse conditions (Torres & Drummond 1997, Arroyo 2002, Villegas et al. 2004). The *sex allocation hypothesis* states that, under certain conditions, parents favour the "least costly" sex to minimise parental investment. Males are the "least costly" sex in raptors exhibiting RSD. Sex allocation may occur when parents are in poor condition, when the food supply is limited, or during adverse weather conditions, (Trivers & Willard 1973). Evidence to support this hypothesis is mixed, with some research documenting male-biased broods when food is limited and/or weather conditions are adverse (Wiebe & Bortolotti 1992, Korpimaki et al. 2000, Ingraldi 2005) and others showing no sex-ratio distortions during adverse conditions (Genovart et al. 2008). In addition, studies have reported demographic factors such as age of parents and laying date to affect brood sex ratios (Leroux & Bretagnolle 1996, Risch & Brinkhof 2002, Ferrer et al. 2009).

In addition to demographic and environmental conditions, sex ratios may also be affected by genetic factors. Inbreeding has been reported to distort sex-ratios by reducing the proportion of the homogametic sex (Worthington-Wilmer et al. 1993, Eldridge et al. 1999). A meta-analysis of published literature compiled by Wilcken in 2001 (cited in Frankham & Wilcken 2006) found a slight overall directional distortion in sex-ratios due to inbreeding. However, there are also data sets that do not show evidence of this distortion (Frankham & Wilcken 2006).

Variation in sex-ratios and its possible consequences to population viability is an important concept in conservation and population ecology (Clutton-Brock 1986, Frankham & Wilcken 2006), and is particularly applicable for small isolated populations (Bro et al. 2000). Extinction risk due to primary sex-ratio distortions is a tangible threat to species with limited population sizes (Gabriel & Burger 1992). It is also an essential parameter and currently a top priority for viability analyses of small populations (Ferrer et al. 2004, 2009; Rossmanith et al. 2006, 2007; Frankham 2010). There is clear evidence that distortion of nestling sex ratios can accelerate extinction in small populations (Brook et al. 2000, Ferrer et al. 2009). For some avian taxa which have recently gone extinct, including the Heath Hen *Tympanuchus cupido cupido* and Dusky Seaside Sparrow *Ammodramus maritimus nigrescens*, the last breeding pairs produced single-sex broods after years of population decline and inbreeding (Avise & Nelson 1989, Simberloff 1988).

The remaining Ridgway's Hawk population is primarily restricted to a small area on the northeast coast of the island (Chapter 3) and evidence suggests that inbreeding is occurring within this small remnant population, possibly at a substantial rate (Chapters 6 & 7). Knowledge of certain aspects of Ridgway's Hawk life history and reproductive traits, including nestling sex ratios, is required in order to assess the species' vulnerability to extinction. This chapter examines reversed sexual size dimorphism in the species from morphometric measurements of live birds, and analyses nestling sex ratios to determine if sex ratio distortion could be placing this small population at increased extinction risk.

8.2 METHODS

8.2.1 Field observations

Breeding pairs of *Buteo ridgwayi* were studied over five breeding seasons (January to July 2005-2009 within Los Haitises National Park on the northeast coast of Hispaniola (see Chapter 2). General nest and pair monitoring methods are detailed in Chapter 2.

Once a nest was found, it was visited every 1-3 days (for easily accessible nests), or every 1-2 weeks (for sites that were more difficult to access) to determine which pairs laid a clutch, and how many reared a chick(s) to fledging. A nest was classified as successful if at least one young fledged. Productivity was defined as the number of fledglings produced per active nest. A nest was considered to have failed if it had been active but subsequently did not produce at least one fledgling. Indications of nest failure were the absence of an attending adult during a 2 to 4 hour observation on successive visits, or the death or disappearance of all eggs or nestlings. Nest contents were identified by viewing through a spotting scope or climbing to nests.

Hawks were banded with unique coloured aluminium identification bands, and morpho-metrics collected (Chapter 2). DNA was collected and extracted as per methods in Chapter 2. Adults were trapped using a bal-chatri noose trap and nestlings were banded on the nests when between 25 and 45 days old (Chapter 2).

8.2.2 Avian molecular sexing

Molecular sexing of the Ridgway's Hawk samples (adults and nestlings) was carried out by PCR amplification of the CHD1 gene. The methods of Fridolffson & Ellegren (1999) with primers 2550F / 2718R were modified as follows.

DNA samples were removed from -20°C storage and incubated in a 37°C water bath for 30 minutes. Polymerase Chain Reactions (PCR) were run on all adult and nestling samples collected in 2005-2007. Genomic DNA was amplified in 10 ul reactions containing 3.7 ul of distilled water, 1.25 ul of PCR reaction buffer (10X TSG), 3.25 ul of 2.0mM MgSO4, 0.25

ul of 10mM dNTPs, 0.25 ul of fluorescently dyed 10uM forward (2550F) and reverse (2718R) primers, 0.05 ul of Taq DNA polymerase (TSG), and 1ul of DNA template (*c.*15ng DNA in TE buffer). PCR reactions were carried out in an Eppendorf MasterCycler^{TM} thermal cycler.

An initial 2 minute denaturing step at 94°C was followed by 30 cycles of 30 s at 94°C, 30 s at an annealing temperature of 50°C, and a 30 s extension step at 72°C. The PCR reaction finished with a final 5 minute extension step at 72°C, and samples were then held at 4°C until taken from the thermal cycler.

Samples were run on a 2% agarose (1.0g agarose powder to 50mL of 1X TBE) gel post-stained with Ethidium Bromide (10uL ETBR per gel). Gels were run at 70V for 75 minutes in order to achieve sufficient band separation to discern males (one band) from females (two bands).

The avian molecular sexing method was based on the fact that male birds are homogametic (ZZ) while females are heterogametic (ZW). This method involved PCR amplification of two conserved chromo-helicase DNA binding (CHD1) genes found on all avian sex chromosomes. The CHD1-W gene is only found on the W chromosome and therefore unique to females whereas the CHD1-Z gene is found on the Z chromosome and expressed in both males and females. Tests used PCR with single primer sets that amplified homologous sections of the two genes. When examined on a 2% agarose gel, male Ridgway's Hawks showed a clear single band for the CHD1-Z gene at 600bp, while females showed two clear bands at the CHD1-Z gene (600bp) and for the CHD1-W gene at 350bp (Figure 8.1).

8.2.3 Data analysis

Mann Whitney *U*-tests were used to compare morphometric measurements between adult males and females. Binomial tests were used to test whether nestling sex ratios (number of males/number of females) deviated significantly from a 1:1 ratio for each year 2005-2008, and for all years combined.

8.3 RESULTS

8.3.1 Sexual dimorphism

Adult female Ridgway's Hawks were significantly greater in size for 7 of the 12 morphometric variables measured (Table 8.1), confirming reversed sexual size dimorphism for this species. Females were *c.*25% heavier than males on average. There was no overlap, with all females weighing ≥ 352g and all males weighing ≤ 323g. Wing chord, tarsus width and culmen were all highly significantly different, with very little overlap between females and males (Table 8.1). Skull width showed a trend toward differentiation between the sexes (p=0.07, Table 8.1). There was no significant difference in size between males and females for bill width, tarsus length, middle toe length, and middle toe claw (Table 8.1).

8.3.2 Nestling sex ratios

Sex was determined for 103 nestlings (42 male, 61 female) from 63 broods between 2005 and 2008 (Table 8.2). Nestling sex ratios (M:F) ranged from 1:1.25 in 2005 to 1:1.90 in

2007 (Table 8.2) and in each year were female biased. None of the years exhibited significant deviations from 1:1 (Table 8.2) but statistical power was limited due to the unavoidably small sample sizes. However, an overall trend in favour of females was evident when all years were combined (Table 8.2).

The majority of broods with two or more nestlings contained mixed sexes (25/38, 65.7%; Figure 8.2). There were greater than twice as many all-female broods (9/13) as all-male broods (4/13) for all seasons combined (Figure 8.2). In addition, there were almost twice as many nests with a single female nestling (16/25) compared to a single male nestling (9/25; Figure 8.2).

8.4 DISCUSSION

8.4.1 Reversed sexual dimorphism

Measurements of live birds during the current study verified reversed sexual size dimorphism in Ridgway's Hawk, as initially reported from museum specimens by Wiley & Wiley (1981). Females were *c.*25% heavier than males on average, and had significantly larger skulls, wings and tails. Sexual dimorphism is typical of the genus *Buteo* with many species showing varying levels of reversed dimorphism (Ferguson-Lees & Christie 2001). There also appears to be a trend for insular species to exhibit higher rates of dimorphism than mainland *Buteos*. Two island *Buteos*, the Galapagos Hawk *B. galapagoensis* and the Hawaiian Hawk *B. solitarius* exhibit the highest levels of reversed sexual dimorphism within the genus, with females being ≥30% larger in mass than males (Paton et al. 1994).

The Red-shouldered Hawk *Buteo lineatus* is the closest taxonomic relative to Ridgway's Hawk (Amaral et al. 2009). Female *B. lineatus* are *c.*21% heavier than males, females weighing 700g and males weighing 550g (Dykstra et al. 2008). This is a slightly smaller proportion than the 25% difference in weight for *B. ridgwayi*.

There were no significant differences between male and female Ridgway's Hawks in tarsus length, middle toe length, middle toe claw, or bill width. Although males are *c.*25% lighter than females, and smaller in other physical traits including skull length, wing and tail length, they have retained similar sized talons, claws, tarsus length, and bill width. For birds of prey, these are morphological traits that are important for hunting. In terms of hunting capability, this may make males more efficient hunters; being smaller and lighter for easier maneuverability within forested areas, yet retaining ample sized hunting morphology including long legs, talons and claws for catching prey, and a wide bill for retaining, killing or ripping larger prey.

Ridgway's Hawk exhibits reversed sexual size dimorphism. Sexual dimorphism in raptors can promote sex-ratio distortion due to environmental and/or social factors (Korpimaki et al. 2000, Ingraldi 2005), therefore, Ridgway's Hawk are vulnerable to these influences on nestling sex ratios.

8.4.2 Nestling sex ratios

The results of the present study suggest there is a weak but consistent sex ratio bias toward females. Deviations from parity can be due to reproductive-related stresses on the population in the form of food limitations, contaminants in the immediate environment (Erikstad et al. 2009), continuous stresses from adverse weather, or genetic-related problems. The results from a concurrent study of food provisioning rates (Chapter 5) suggest that food availability was not a limiting factor on reproductive success.

A difference of 25% in body mass between male and female Ridgway's Hawk's is likely sufficient enough to generate a sex bias due to differential parental investment, with parents investing in females. Food resources were abundant during the study period (Chapter 5) and parent body condition did not appear to be compromised during the study (author pers. obs). As a result of this resource abundance, Ridgway's Hawk may be investing in the 'more expensive sex'. Supplementary feeding of critically endangered Kakapo *Strigops habroptila* produced a bias in chick production toward males, which in Kakapo are the more costly sex (Clout & Merton 2002).

Ferrer et al. (2009) documented a sex ratio distortion for the endangered Spanish Eagle *Aquila adalberti* that was related to a decrease in the mean age of breeding birds with younger breeding birds producing significantly more male biased broods. There was no evidence during the current study to suggest that there were a large number of immature or young breeding pairs, although this is mainly due to the small sample size of banded individuals and limited knowledge on age history of the breeding population. However, with banded nestlings reaching breeding age in the next few years it is recommended that pairs continue to be monitored to determine juvenile and adult survival and any age related nest productivity.

Although little is known about natal dispersal in Ridgway's Hawk, it is generally accepted that female raptors disperse further than males (Newton 1979). The *differential dispersal hypothesis* (Gowaty 1993) states that, if sexual differences in natal dispersal lead to varying degrees of competition between parents and young, sex ratios should be skewed toward the sex that disperses the farthest. Although it appears that natal dispersal in both sexes is minimal and less than 3km (Chapter 4), there may be different levels of philopatry exhibited between male and female Ridgway's Hawks. A better understanding of natal dispersal and juvenile movements of Ridgway's Hawk are recommended as an important component of any future research for this species.

The occurrence of inbreeding within the remaining population of Ridgway's Hawk (Chapters 6 & 7) could be affecting nestling sex ratios. Although directional distortions in sex ratio do not appear to be a consistent signal of inbreeding depression, small random populations can exhibit severe distortions from autosomal sex-limited alleles that have drifted in isolated populations (Frankham & Wilcken 2006). There is evidence that 18% of potential random pairings of Ridgway's Hawk could be inbred (Chapter 7). Inbreeding can potentially distort sex ratios by reducing the proportion of the homogametic sex (Worthington Wilmer et al. 1993, Eldridge et al. 1999). Therefore, we could expect distortions toward female-biased broods within inbred pairings of Ridgway's Hawk. The four breeding pairs that showed evidence of being inbred produced 7 chicks, 5 of which were female. Three broods consisted of 1 female chick each, and 2 broods were mixed (one male, one female; Appendix 7.2).

8.4.3 Conservation implications

The trend toward a female-bias in nestling production could be an encouraging sign for Ridgway's Hawk. This could suggest that food resources are more than adequate for the number of breeding pairs currently nesting in the area, that adults are in relatively good physical condition during the breeding episode, and that no other obvious environmental stresses are promoting "cheaper" sex allocation by the parents. There are other significant stresses on the population including habitat loss and direct human persecution (Chapter 4). However, these stresses do not, for the moment, appear to be negatively affecting nestling sex ratios in Ridgway's Hawk.

The potential concern would be if the trend toward female directional distortion was being caused by inbreeding within the population. This is a possibility, as inbreeding may be potentially occurring at a fairly substantial rate (Chapter 6.4.2). Nestling sex ratio should be monitored closely in the future. The mechanisms of sex ratio distortion are complex, and others studies of endangered species have also strongly recommended that monitoring of fledgling sex ratios be a required component of conservation strategies for small vulnerable populations (Ferrer et al. 2009).

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Table 8.1 Mean ± SD (range) for twelve measurements from 20 adult female and 15 adult male Ridgway's Hawks. Size dimorphism indices (SDI) were calculated as the mean of the female measurement divided by the mean of the male measurement minus one. All variables are reported in mm except for body mass (g).

Measurement	Male	Female	SDI	P*
Body mass	310.5 ± 11.0 (286 - 323)	402.6 ± 24.6 (352 - 450)	0.30	**0.00**
Wing chord	228.3 ± 13.8 (200 - 244)	250.9 ± 7.6 (226 - 260)	0.11	**0.00**
Skull length	44.3 ± 2.0 (40.3 - 47.6)	45.6 ± 1.9 (40.9 - 49.7)	0.03	**0.04**
Skull width	36.9 ± 2.6 (34.4 - 40.6)	37.8 ± 3.3 (35.2 - 40.9)	0.02	0.07
Bill culmen	17.0 ± 1.4 (14.9 – 19.1)	18.5 ± 1.2 (16.4- 21.0)	0.08	**0.01**
Bill width	13.3 ± 3.4 (8.6 - 16.3)	13.5 ± 3.4 (9.1 - 16.7)	0.01	0.35
Bill depth	13.4 ± 1.0 (12.1 - 15.6)	13.9 ± 0.8 (12.5 - 15.2)	0.03	**0.04**
Tail length	147.7 ± 9.0 (125 - 161)	153.8 ± 6.8 (139 - 164)	0.04	**0.03**
Tarsus length	73.4 ± 3.3 (68.3 - 78.0)	75.2 ± 3.8 (69.7 - 80.9)	0.02	0.12
Tarsus width	6.2 ± 0.8 (5.4 - 7.4)	7.0 ± 0.8 (5.8 - 8.1)	0.11	**0.00**
Middle Toe	29.9 ± 2.3 (26.1 - 34.0)	31.0 ± 2.4 (27.2 - 35.5)	0.04	0.17
Middle toe claw	16.7 ± 1.2 (14.5 - 17.7)	17.4 ± 1.1 (15.5 - 18.9)	0.04	0.11

* Mann Whitney U-test

Table 8.2 Observed annual sex ratios of Ridgway's Hawk nestlings from 2005-2008.

Year	Males	Females	No. broods	Sex ratio (M : F)	% Males	P-value*
2005	8	10	12	1 : 1.25	44.4	0.82
2006	10	15	14	1 : 1.50	40.0	0.42
2007	10	19	19	1 : 1.90	34.5	0.12
2008	14	17	18	1 : 1.21	45.2	0.72
All years	42	61	63	1 : 1.38	42.0	0.09

*Binomial test

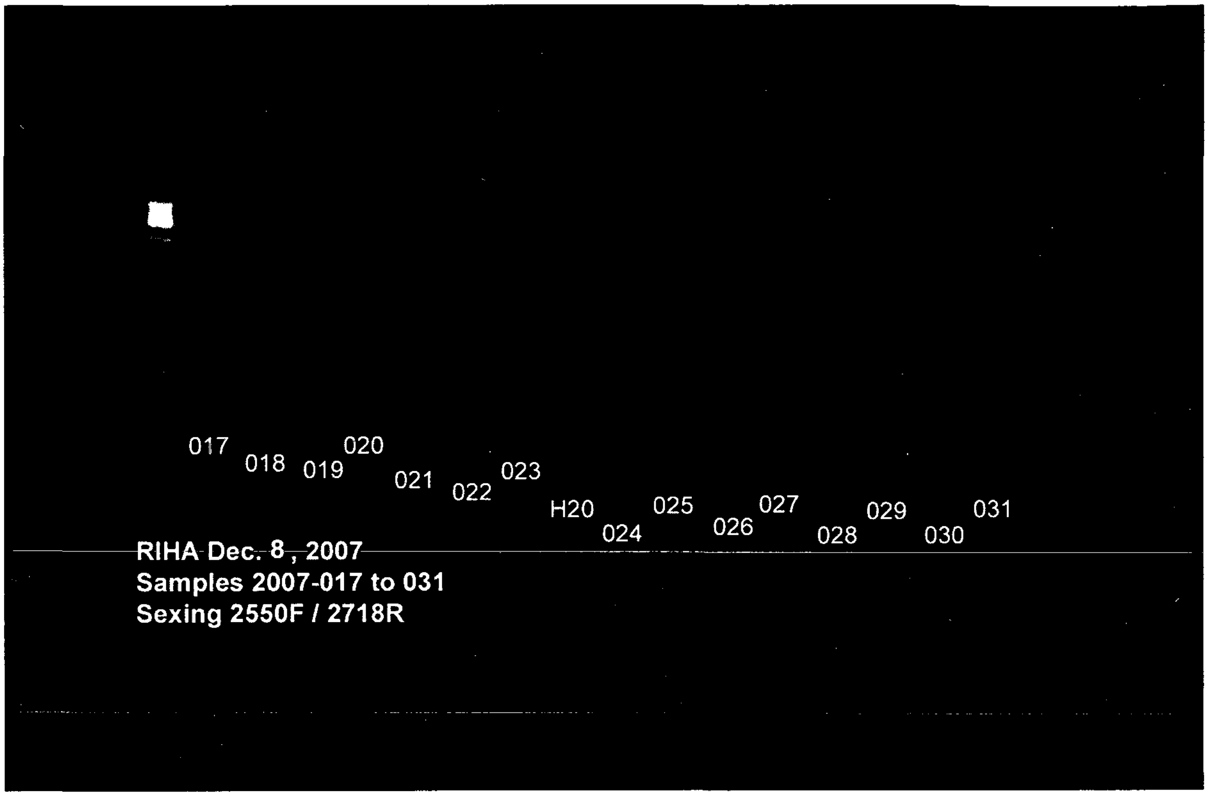

Figure 8.1 Electrophoresis gel showing results of CHD1 gene sexing for Ridgway's Hawk *Buteo ridgwayi*. Double bands are females. Birds 28, 29 and 31 were adult females. Bird 30 was an adult male. All others were nestlings.

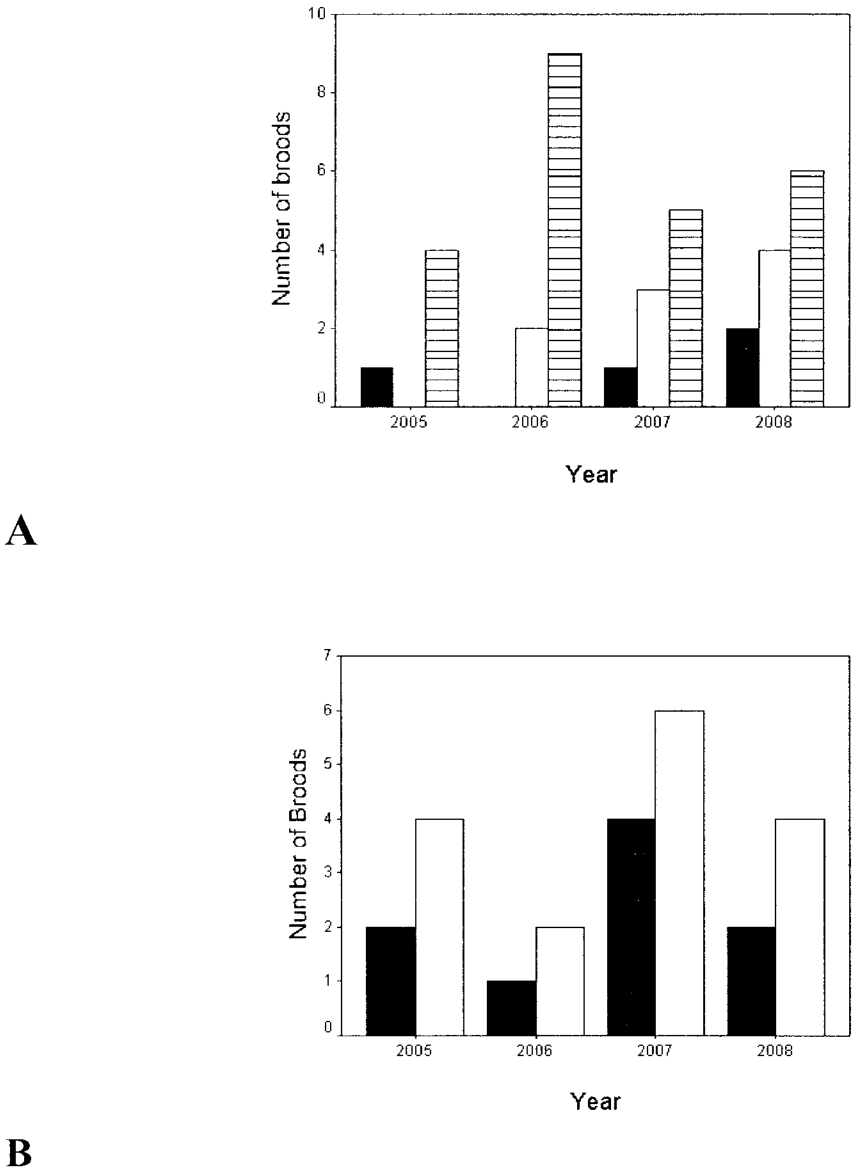

Figure 8.2 Number of Ridgway's Hawk broods per year with mixed sex nestlings (striped bar), all female nestlings (white bar), and all male nestlings (black bar). **A** - Broods with two or more nestlings and **B** - Broods with only one nestling.

Chapter 9

CONCLUSIONS AND CONSERVATION RECOMMENDATIONS

"The beauty and genius of a work of art may be reconceived, though its first material expression be destroyed, a vanished harmony may yet inspire the composer; but when the last individual of a race of living things breathes no more, another heaven and another earth must pass before such a one can be again." William Beebe (1906)

A major motivation for this thesis was to improve management planning for the species by providing information on:

- The current population distribution and trend in numbers of Ridgway's Hawk;
- The levels of genetic variation within the remaining population;
- The productivity of remaining breeding pairs and;
- The current threats and risks presented to the extant population.

This research was carried out in part to provide conservation recommendations to ensure the species' future survival.

9.1. POPULATION STATUS

Historical sightings and museum specimens indicate Ridgway's Hawk was widespread yet rare during the last century, and most locally common within coastal low and mid-elevation forests. The global population of Ridgway's Hawk has declined throughout its range and is now limited to Los Haitises National Park in the northeastern Dominican Republic.

The results of this 5-year study revealed some positive findings for viability of the Ridgway's Hawk population, but also several serious causes for concern.

9.1.1 Positive findings

1. Relatively high genetic diversity.

Although it is difficult to compare heterozygosity levels among different studies, species, and microsatellites that have experienced different evolutionary scenarios, Ridgway's Hawk appears to have relatively high levels of remaining genetic diversity. Caution is required though as a considerable percentage of nestlings (40%) are being produced by a smaller subset (25%) of the breeding pairs and the species has undergone a recent rapid decline in population size and distribution. Since allelic diversity is reduced faster than heterozygosity during bottlenecks, this can result in a transient elevated level of heterozygosity. Therefore, heterozygosity of the population may be in fact much lower than this study reports.

2. Relatively high productivity, and low rate of infertile eggs and embryonic death.

Nest success and productivity of the remaining population of Ridgway's Hawk were comparable to, and in many cases greater than, that of other similar-sized neotropical raptors. Low reproductive productivity does not appear to have been a contributing factor to the species' decline. There was no evidence to-date for compromised productivity due to infertility or embryonic death.

3. Adequate prey supply within Los Haitises National Park.

The karst topography and climate of Los Haitises have produced a reptile community high in abundance and diversity (Glor et al. 2001), which in turn provided an abundant prey base for Ridgway's Hawk. This allowed for relatively high nest productivity and recruitment to the population.

4. Relatively high pair density within Los Haitises National Park.

The karst topography of Los Haitises has provided a situation whereby the actual area of usable habitat extends up the sides of the mogotes, substantially increasing the amount of habitat beyond that seen on a two-dimensional map. This, in conjunction with high prey availability, has allowed Ridgway's Hawk to persist in relatively high densities within the remaining habitat of Los Haitises. Otherwise, the global population of Ridgway's Hawk would likely be even closer to extinction.

9.1.2 Causes for concern

1. Limited global range, low censused and effective population sizes, and a decreasing *population trend.*

The population range of ~1600 km^2 and censused population size of ≤109 breeding pairs is exceedingly low for a vertebrate predator species. An extinction vortex can result when an avian population decreases below a threshold of *c.*110 individuals (Fagan & Holmes 2006). When the effective size of a population is small, such as the estimated 15-18 breeding pairs of Ridgway's Hawk, genetic diversity decreases with the loss of each single individual (Nei et al. 1975). The Ridgway's Hawk population distribution and trend is still declining.

2. *High mortality rate of nestlings and adults due to human activities and persecution.*

Human persecution, both confirmed and highly suspected, accounted for 60.7% of nest failures from 2005-2009. Banding and genetic information indicated a high rate of mate replacement. This turnover rate does not appear to be caused by divorce, but by mortality, as no replaced birds were re-sighted in subsequent years. There was substantial evidence of high persecution of adults by local villagers, supported by this high turnover rate. From 2003-2005, 13 adult hawks were known to be killed because of the misconception that they prey significantly on poultry (Thorstrom et al. 2005). One villager claimed to have killed more than 100 hawks in a ten-year period. The misconception that Ridgway's Hawks are a substantial poultry predator has led to the unfortunate persecution of *B. ridgwayi* and is the most probable reason, along with habitat loss, for the species' rapid population decline.

3. *High variation in reproductive success among pairs.*

Twenty-five percent of the nesting territories monitored during the present study produced

40% of the fledglings. Loss of these territories, through slash-and-burn agriculture could lead to a rapid decline of the species toward extinction. Loss of these productive territories could occur over a single breeding season if an uncontrolled fire were to pass through these territories. Urgent measures are required to protect remaining forest in these productive territories and to improve overall productivity in other territories by reducing Hawk persecution and uncontrolled burning.

4. *Strong evidence of inbreeding and a recent population bottleneck*

The analysis of genetic variation revealed several genetic indicators that inbreeding was occurring within the population. The majority of microsatellite loci exhibited both deviations from HWE and linkage disequilibrium. Other potential causes of these deviations, such as null alleles or population structuring, were assessed but ruled out leaving inbreeding the most likely cause. In addition, positive inbreeding coefficient values were found in 9 of the 11 sampled loci.

The occurrence of inbreeding was further supported by a genetic relatedness analysis which found that four of eight sampled breeding pairs were inbred. Additional analysis determined that 18% of potential random pairings would be between individuals related at a level equivalent to that of half-siblings or greater. This represents a tangible threat to the species, particularly if the species continues to decline in population size and range due to other direct threats such as habitat loss and persecution.

Although there was no evidence of compromised productivity or survival linked to inbreeding, if a possible increase in homozygosity occurs in nestlings from inbred pairings, this could be a serious concern in the near future. Although not reported in this thesis, the author would like to note the following anecdotal information collected on the nestlings of the sampled breeding pairs. The nestlings from four sampled inbred pairings appeared to exhibit more homozygous genotypes than nestlings from three pairings that were not inbred. On average, the seven nestlings from inbred pairings were homozygous for 5.0 (±1.1) of the 11 loci, with three nestlings being homozygous for ≥6 of the 11 loci. By comparison, four nestlings produced by three non-inbred pairings were homozygous for an average of 2.7 (±0.7) of the 11 loci, and no nestlings were homozygous for >4 out of the 11 loci. This sample size is too low for any statistical analysis. However, since increased levels of homozygosity have been associated with increased inbreeding depression and reduced survival (Blomqvist et al. 2010), this potential toward homozygosity in nestlings from inbred pairs needs to be investigated and considered during management planning.

Each of these above concerns on it's own would be considered a serious threat to the population viability of Ridgway's Hawk. With all acting concurrently on this small population, the threat of extinction becomes even more imminent.

9.2 CONSERVATION RECOMMENDATIONS

9.2.1 Protection of Ridgway's Hawk within Los Haitises National Park (LHNP)

The future survival of Ridgway's Hawk in its natural environment depends on the effective management and protection of Los Haitises National Park.

9.2.1.1 Effective delimitation and enforcement of LHNP boundaries

Los Haitises National Park is a "paper park" with no clear boundaries (Geisler et al. 1997). It has experienced a massive, uncontrolled immigration since the 1980s. As of 1994, 5,500 new households were estimated to be living in 11 villages within or along the edges of the Park (Stycos & Duarte 1994). The current situation has been complicated by the repeated expulsion and re-colonisation of the Park, creating resentment and a sense of "entitlement" in the local people. This has been further complicated by the commercialisation of root-crop cultivation, managed by local people with political power. Despite this intense pressure, the author has observed that the conscientious application of National Park regulations by a handful of Park Guards and Administrators can make a profound difference. In 2005 when the author began research on Ridgway's Hawk, the western half of the National Park was administered by a dynamic individual, and a single Park Warden was conscientiously applying Park regulations on the western side of the National Park near Los Limones. No new areas of forest were slash-and-burned within that area in 2005. In 2006, the Administrator and Warden were replaced after a change in government staff following a national election, and large areas of the forest cover in that area were subsequently cut and burned (author pers. obs.). Although solutions to this complex situation are beyond the scope of this thesis, two initial actions are recommended:

1. An awareness campaign should target the National Parks and government of the Dominican Republic regarding the significance of Ridgway's Hawk as a Hispaniolan endemic on the brink of extinction.

2. A national workshop should be held that includes all stakeholders in conservation of Los Haitises National Park, including local communities, the Subsecretaría de Estado de Areas Protegidas y Biodiversidad, the Secretaría de Estado de Medio Ambiente y Recursos Naturales, conservation and development NGOs, and tourism operators. Although Ridgway's Hawk could play a role as a flagship species, preserving the ecological integrity of the karst rainforest through the effective delimitation and management of the National Park should be the central theme of the workshop.

9.2.1.2 Sustained community education and awareness programmes

The misconception that Ridgway's Hawks are significant poultry predators has led to the widespread persecution of *B. ridgwayi*. This misconception is fuelled by confusion with the larger, sympatric Red-tailed Hawk *B. jamaicensis* which does kill chickens.

An awareness campaign initiated by The Peregrine Fund and the Sociedad Ornitologica de Hispaniola produced a poster and series of community theatres from 2005-2007. From 2005-2008, the author and Wildlife Preservation Canada carried out a community awareness program with local "landowners" that were farming within the Park. This was extremely simple and inexpensive. Most people were unaware of the uniqueness and rarity of Ridgway's Hawk and were genuinely interested. Although some people's views were inflexible, the majority of farmers began at least protecting hawks and their nesting trees. In three instances, local people protected nestlings that had fallen from nests until the nest could be repaired and the nestlings returned.

However, these community awareness programs have not continued. A small-scale yet consistent awareness program, based on successful community programs in the Lesser Antilles (Butler 2000) should be implemented. An annual visit to 10-12 villages and 8-10 main schools around Los Haitises, could make a significant impact on reducing persecution of Ridgway's Hawk. Target audiences could begin with those groups most likely to come into daily contact with hawks and nests, primarily local farmers and schoolchildren.

9.2.1.3 Stop the burning

During this study, the author has observed nesting Ridgway's Hawks and local farmers co-existing within the same valleys. Local landowners can be convinced of the fact that the Ridgway's Hawk will eat rats, and are thus of benefit to crops. The remaining fragmented karst rainforest of Los Haitises is productive, and as long as native rainforest remains on the tops of mogotes, there is sufficient reptile prey for hawks to feed their nestlings and farmers can continue to produce crops in the fertile valleys below. However, the traditional practice of burning after cutting has a devastating effect on the remaining patches of forest. Even if it is too difficult on a political scale to reduce the level of agricultural within the Park, eliminating burning as a traditional practice would allow remaining forest patches on the mogotes to continue providing habitat for Ridgway's Hawk and other endemics.

9.2.1.4 Establish simple population monitoring and nest protection program

A simple population monitoring and nest protection program should be implemented in Los Haitises. Training local people to collect basic monitoring data on known nesting pairs, following established successful models (Mulwa et al. 2007) would provide basic information on nest success and population trends, but also provide a local community-based form of control and nest protection that would integrate communities within conservation efforts.

9.2.2 Future field research

9.2.2.1 Survey remaining potential population sites

There is very little chance of any viable populations remaining outside of Los Haitises. A few birds or pairs may remain in fragmented forest patches on the Samaná Peninsula, on Isla Beata or in the Cordillera Oriental but these populations would not be likely to persist beyond the current lifespan of the birds. Since gene flow rates as small as one immigrant per generation can counteract the effect of genetic drift in small populations (Nei et al. 1975), translocations of even one individual (nestling) from these areas could help retain genetic diversity within the population. If a handful of Ridgway's Hawk still exist outside of Los Haitises, they need to be discovered and either protected *in situ*, or brought in to captivity so that their genetic potential is not lost.

9.2.2.2 Population monitoring and survival of fledglings and adults

During the current research from 2005-2009, 37 adults (21 female and 16 male), 1 juvenile female, and 61 nestlings (36 females and 25 males) were banded. A simple monitoring scheme should be implemented to follow survival rates of these banded individuals. Mortality rates can be compared to productivity (this study) to refine population trends. Training local people to carry out the monitoring would help increase awareness and species' ownership within local communities.

9.2.2.3 Additional causes of mortality

An area of research related to nesting success that requires immediate study is the potential role of disease in nestling deaths. The prevalence and types of disease organisms affecting Ridgway's Hawk are completely unknown. West Nile Virus is known to have been spread to Los Haitises in 2002 (Komar et al. 2003) but the effect of this disease on Ridgway's Hawk is unknown, although does not as of yet appear to have been severe. Very small populations are highly vulnerable to exotic disease, and this is an area of knowledge for which conservation scientists are completely unprepared at the moment to deal with for this critically endangered raptor.

9.2.3 Compare contemporary to historical DNA

Comparing the DNA of contemporary birds to historical specimens is the most reliable way to determine the rate of loss of genetic diversity that has occurred within the population during the recent population bottleneck. A list of museum specimens has already been compiled by the author.

9.2.4 Model Population Viability

Enough knowledge now exists to carry out a preliminary PVA (Seal 1993) to identify threshold levels and extinction scenarios for Ridgway's Hawk. Knowledge gained from this modelling exercise would better prepare conservation managers in conservation planning for the species. A PVA would also help identify areas of knowledge which are currently lacking.

The author highly recommends a PVA workshop be facilitated by the IUCN/SSC (International Union for the Conservation of Nature/Species Survival Commision) Conservation Breeding Specialist Group (CBSG) which represents the world expertise in modelling viability of populations of highly threatened species under a range of scenarios. These workshops, organized and hosted by the IUCN/SSC CBSG, have been carried out world-wide on hundreds of threatened species, including insular avian species, and involve participation by international and local NGOs, stakeholders, and other local organizations (IUCN/SSC CBSG 2010).

An advantage to such a workshop would be the bringing together of all stakeholders in one location to discuss conservation plans and goals for Ridgway's Hawk. "Through this methodology, the conservation decision-making process is improved with considerably greater local ownership of the recommendations that are developed and presented by the participants themselves..." (IUCN/SSC CBSG 2010). As part of this workshop, the participants would be expected to develop a detailed management and research plan, with full reports being distributed, reviewed and finalized in 2-3 months (IUCN/SSC CBSG 2010). Rapid dissemination of recommended conservation actions from a consensus of all involved parties is urgently needed for Ridgway's Hawk.

9.2.5. Establishment of a captive population

At the moment there is no need yet for a large-scale captive breeding and re-introduction program for Ridgway's Hawk, particularly if it were to take away from attempting to save the species within its last remaining habitat of Los Haitises. However, since the entire world population is located within this one small area, the establishment of a captive population is highly recommended for the following reasons:

1. A single small population is vulnerable to stochastic events.
2. The remaining population is vulnerable to human disturbance.
3. A properly managed captive population could retain current genetic diversity before inbreeding increases in the wild population.
4. It is unlikely that maintenance of the population, even at its current size, would result in long term survival of the species.

Hawk husbandry techniques are well known and raptors are relatively easy to breed in captivity compared to other avian taxa. Based on the ecology of the species, the author has no reason to believe that Ridgway's Hawk would be particularly difficult to breed in captivity.

Selection of founder nestlings for the captive population should be carried out with two main priorities in mind: First, the selection process should identify the most genetically divergent individuals to capture as much of the remaining genetic diversity as possible. Second, the selection of nestlings should focus primarily on breeding pairs in areas that would otherwise face a high probability of nest failure, and therefore would have little to lose. With genotypes of a considerable number of birds now known, and the knowledge of the highly productive areas within Los Haitises, this selection process could be done relatively easily.

9.2.6. Translocations

Conservation organisations have begun translocating juveniles from Los Haitises to establish peripheral safety net populations on private lands outside of the National Park ; Punta Cana on the eastern tip of the Dominican Republic, and at La Herradura in the Cordillera Oriental. Four juveniles were relocated in Loma La Herradura in the Cordillera Oriental in 2008, and three juveniles released in Punta Cana in 2009.

While all action to save Ridgway's Hawk should be attempted, translocations should be designed in order to avoid any harm to the remaining population in Los Haitises and should not detract from the main goal of preserving this natural population. Available resources should remain focused on stabilising the Los Haitises population. Potential translocation sites should have a sufficient reptile prey base and be areas where hawks will not be persecuted.

If these conditions are met, translocations of nestlings to establish new safety net populations should be a relatively low risk activity. The current research has shown that pair productivity in Los Haitises is high but that 61% of nests from 2005-2009 failed due to human persecution. Selecting nestlings for translocation from areas that would otherwise face a high probability of nest failure would have little to lose. Most fledglings currently have no habitat to disperse to, as all of the remaining forest cover in Los Haitises is currently saturated. Hacking nestlings to other fragmented forest could provide a catalyst for local awareness, and habitat restoration and protection outside of Los Haitises. Establishing safety net populations, as long as it does not take resources away from protection of the remaining population in Los Haitises, could increase the global population.

9.3 A FINAL WORD....

Although this research has revealed several causes for concern for the future survival of the Ridgway's Hawk population, the results do provide some hope. The relatively high productivity and adaptability to using degraded forest for nesting are likely the two main reasons that Ridgway's Hawk still persists today. Although inbreeding is occurring within the population, there is no strong evidence as yet of inbreeding depression; although caution is warranted as there may be a potential trend toward increased homozygosity in nestlings of inbred pairings. As a safety net for the population's current genetic diversity, the establishment of an initial captive population is highly recommended.

More intensive management of the population will most likely be required in the near future. If sensible conservation measures are taken to protect the remaining coastal karst rainforest within Los Haitises National Park, the remaining wild population could stabilise. If Ridgway's Hawks are provided with a protected forested area, free from direct human persecution and with sufficient reptile prey densities, the species could recover. However, these measures must be taken during the next few years, before the remaining population declines much further.

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