Ecology and conservation of a diurnal raptor community within a protected area in northwestern Peru

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Abstract

Birds of prey are difficult to study and the status and distribution of many species is poorly known. As top predators usually occurring at low densities, raptors may be particularly sensitive to habitat degradation. Conservation of raptors might be vital to prevent further loss of species and ecosystems. Between April and December in 2008 and 2009, raptors and associated habitat data were surveyed using a distance sampling transect method in 70 randomly selected one square kilometre plots in the Cerros de Amotape National Park, the Tumbes National Reserve and buffer areas within the North West Biosphere Reserve in Peru. A total of 1261 detections of 19 diurnal raptor species were recorded.

I examined community structure, diversity across land uses and relationships between abundance and niche attributes within species. Abundance and richness were highest outside protected areas and lowest in the national park. A Canonical Correspondence Analysis (CCA) of raptor species and habitat variables ordinated them according to latitude, elevation, percentages of vegetation cover, and, in some cases, individual tree species.

I used logistic regressions (GLMs) to obtain habitat distribution models for eleven raptor species. Twenty eight habitat models were obtained and twelve habitat variables were included. Best models included measured percentage of vegetation cover at different strata, elevation and latitude. My findings suggest that vertical structure of forested areas is of particular importance for raptors in extreme northwest Peru.

Density and population size estimates were calculated for 15 species using distance sampling line transect counts. Densities were stratified by time of detection (morning or afternoon) and by habitat type. Flying birds were included in the analysis. For all but two species, density estimates were higher in the morning than in the afternoon. Absolute density was higher than 1 individual km^{-2} for three species and for seven species it lay between 0.34 and 0.86 individuals km^{-2}. Some species showed a marked preference for particular habitat types.

I used generalized additive models (GAMs) to examine the relationship between the occurrence of six diurnal raptors and species diversity and abundance to vegetation structure, elevation and cattle 'density' in 39 km^2 plots within my study area. Percentage of vegetation cover 5-15 m above the ground was the most important feature influencing the distribution of most species, including the rarer ones. Raptors responded differently to cattle density: Presence of species that foraged in open habitats increased with cattle density, while presence of range restricted or declining species decreased.

Conservation efforts of raptors in extreme northwest Peru should also be conducted in areas outside the North West Biosphere Reserve by protecting remaining forests. Moderate cattle densities can benefit some species and help maintain a high raptor diversity in the study area. However, this activity should be strictly monitored so further fragmentation of forests and damage to vegetation structure is significantly reduced particularly inside the Tumbes National Reserve.

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Chapter 1: An introduction to tropical raptors: Ecology, status and study

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1.1 Raptor diversity and distribution

There are serious disputes on the number of species considered as diurnal raptors (Sibley and Monroe 1990; Fergusson-Lees and Christie 2005), although most authors agree that this group includes five families: The Cathartidae (New World vultures), Pandionidae (Osprey), Accipitridae (kites, eagles, vultures and hawks), Sagitaridae (Secretarybird), and the Falconidae (caracaras, forest falcons, pygmy falcons, falconets and true falcons) (Fergusson-Lees and Christie 2005; Remsen et al. 2011). In all, these five families encompass a range of 292 to 338 species that are found in all continents, except for Antarctica and in many oceanic islands around the world (Amadon and Bull 1998; Bildstein 2004; Fergusson-Lees and Christie 2005). Differences in the number of species are accounted by the status of some raptor subspecies that are considered full species (eg. the Sharp-shinned Hawk -*Accipiter striatus*) (Fergusson-Lees and Christie 2005; Remsen et al. 2011); species that are treated as conspecific (Variable Hawk –*Buteo polyosoma* with Puna Hawk –*Buteo poecilochrous*) (Schulenberg et al. 2007; Remsen et al. 2011) or separated (Cabot and de Vries 2003), species with uncertain status (eg. the Altai Falcon -*Falco altaicus*) (Eastham and Nichols 2002; Wink and Sauer-Gurth 2004) and new species being recently discovered (Cryptic Forest Falcon -*Micrastur mintoni*) (Whittaker 2002).

Although the exact number of diurnal raptor species is still controversial, it is widely acknowledged that approximately 80% of species occur totally or partially in tropical regions (Kennedy 1986; Bildstein et al. 1998), and that the most important regions for raptor conservation lie within the tropics (Thiollay 1994). There are only nine countries with 70 or more diurnal raptor species (Peru, Colombia, Venezuela, Ecuador, Tanzania, Ethiopia, Kenya, Sudan and Uganda) and all of them are within the tropical regions of the world (Bildstein et al. 1998; Schulenberg et al. 2007; GRIN 2012).

1.2 Morphology

Strong hindlimbs and sharp curved beaks used to subdue and kill large prey are the most characteristic anatomical features of the Falconiformes, and along with wing morphology these features can be used to express ecological separation and/or overlap, sexual and age dimorphism, habitat selection and hunting strategies within families and species (Biggs et al. 1977; Mendelsonhn et al. 1989; Ward et al. 2002; Fowler et al. 2009). There are several differences in the foot, beak and wing structure of Accipitridae and Falconidae. Accipitridae have stronger and more robust tarsi, toes and claws and their feet are more adapted to capture and kill prey (Schoener 1984; Fowler et al. 2009). *Accipiter* species, a predominantly tropical group that mainly predates on birds have large and thin toes equipped with long and slender claws. In piscivorous taxa within the Accipitridae and the Osprey (*Pandion haliaetus*) in the Pandionidae, claws are used to impale fish and are particularly large and curved (Fowler et al. 2009).

Among the Falconidae, *Falco* species have robust feet and large toes (but short claws) that facilitate striking and grabbing fast moving prey, while caracaras and forest falcons´s hindlimbs are more suited for searching and capturing prey in the ground (Cade 1982; Robinson 1994; Ward et al. 2002).

Raptor families and species also differ in cranial morphology, probably as a consequence of dietary preferences. Falcon species primarily use their beaks to kill prey by severing the spinal cord at the base of the skull and hence their beaks have developed tomial teeth and cutting edges in the maxilla (Cade 1982; Hertel 1995). Scavengers (old and new world vultures) feed on large dead prey and have developed skull structures that facilitate ripping and twisting big pieces of meat from carcasses (Hertel 1995).

In the Falconiformes, proportions of wings and body mass are related to particular hunting strategies and different flight styles. Wing loading (weight per unit of wing area) is of particular importance in influencing flying and hunting mode (Jaksic and Carothers 1985; Kirmse 1998). Species will also vary their hunting strategies depending on prevailing weather conditions, topography and prey availability in their territories (Barnard 1986; Buchanan 1996; Mueller et al. 2004).

1.3 Reversed sexual dimorphism

Raptors are an exceptional group among birds because they present reversed sexual dimorphism meaning that for most species females are larger than males. In addition, size differences between genders are generally greater in

species that capture large prey and in ornithofagous taxa like *Accipiter* species (Amadon 1975; Snyder and Willey 1976; Boal and Mannan 1996).

Several theories dealing with ecological, physiological, anatomical and behavioral adaptations have tried to explain reversed sexual dimorphism but, so far, none has gained general acceptance (Bildstein 1992; McDonald et al. 2005). Probably the most extended is the one stating that differences in size within a couple allows the capture of differentiated prey, expanding the range of predatory items and broadening the food niche which in turn maximizes dietary intake. This might be particularly beneficial in times of high food demand (i.e. when the pair has to feed chicks). This theory however does not explain why females are larger than males (Amadon 1975).

Reproductive behavior and physiology may provide some explanations for the increased size of female raptors. Aggressive (and smaller) males have less chance of killing females at early stages of pair bonding and mating. In addition, larger females may be more successful in securing a territory held by a male that is ready to mate by excluding other (smaller) females. In some species, smaller males have proved to be more successful hunters during courtship at low food availability periods and were preferred by females for mating (Olsen and Olsen 1987; Hakkarainen et al. 1996; McDonald et al. 2005). Additionally, egg size, which is relatively large in raptors, might drive evolution of larger females, which in turn might be more successful during brooding given their larger feather sizes (Rahn et al. 1975; McDonald et al. 2005).

1.4 Raptor studies

Raptors are naturally low-density occurring species that usually segregate each other because they compete for food, nesting sites and territories. Additionally many species inhabit remote areas. Forest interior species are secretive and inconspicuous and hence very difficult to detect (Thiollay 1985; Falk and Moller 1988; Katzner et al. 2003). Given these particular features, obtaining large amounts of data or proper sample sizes for meaningful analysis is particularly difficult and time consuming (Bednarz 2007). However, raptors are regarded as charismatic, powerful and mysterious animals and through history many species have been selected as national symbols. This fascination has led to the protection of many raptor species and for this, research and scientific knowledge have proof vital (Cade et al. 1988; Salvador and Ibanez 2006).

1.5 Habitat

The study of the relationships between species and its habitats has been a key question in ecology and has a long tradition because it is usually assumed that species prevail in those habitats they prefer so understanding their response to habitat changes is important for their conservation (Schmutz 1989; Lopez-Lopez et al. 2007; Tapia et al. 2007).

Habitat loss is regarded as the most important threat to raptors, yet for most species little is known on their habitat preferences, on the processes involved in habitat selection or how they respond to habitat loss (Thiollay 1994; Bierregard 1998). Recent habitat studies in Falconiformes have been directed to find correlations between presence of species and environmental variables to

predict its occurrence or to measure the availability of resources required by a species to sustain high rates of survival (Janes 1985; Bustamante and Seoane 2004; Guisan and Thuiller 2005; Tapia et al. 2007). Some studies dealing with habitat use by raptors have made quantitative assessments of species and individuals in particular areas and relate this data to species presence and absence. However species absence from a particular habitat does not mean that this is being avoided and might be a consequence of its availability (Jones 2001; Thiollay and Rahman 2002).

Although usually confounded with habitat use, much less attention is paid to behavioral patterns that condition habitat selection and the use of resources (Jones 2001; Martinez et al. 2003). Behavioral information related to the presence of individual in a given habitat is fundamental to understand habitat selection processes and deserve more attention from researchers. (Jones 2001). The understanding of species (and prey) behavioral responses to environmental changes in times when natural habitats are continuously and irreversibly changing pose an increasing challenge because it requires long periods of field work and because hypothesis are more difficult to prove. Behavioral traits behind habitat selection could help predict species responses to habitat loss and may provide key information for their conservation.

1.6 Migrations

Raptor migrations mostly involve individuals travelling from breeding grounds in the north to summer grounds in the south; however, intra tropical, altitudinal and south to north migrations (particularly in the neotropics) have also been

documented (Bildstein and Saborio 2000; Bildstein 2004; Hoffman et al. 2002). For most species, availability of food resources is the suspected main driver of migration (Fergusson-Lees and Christie 2005).

Approximately 60% of all raptor species undertake some form of annual seasonal migration. Most species follow established flyways along leading lines of particular topographic features connecting land masses, while others migrate in many directions (Bildstein and Zalles 2001; Hoffman et al. 2002; Bildstein 2004). Raptor migration flyways usually allow movements of birds over land and most individuals avoid crossing open water that lead to high mortality rates (Zu Aretz and Leshem 1983; Kerlinger 1985).

The Mesoamerican Land Corridor a stretch of land connecting North and South America is used by almost 5 million raptor individuals that leave their breeding grounds during the boreal autumn and head south. More than 90% of the whole populations of three species (Missisipi Kite –*Ictinia mississippiensis*, Broad-winged and Swainson´s Hawk –*Buteo swainsoni*) and the whole American population of the Osprey are involved in these southward movements (Bildstein and Zalles 2001; Bildstein 2004). Conservation of habitats along migration routes is vital for the survival of individuals during migrations (Bildstein 2004).

1.7 Hunting

Raptors species are regarded as opportunistic predators and composition of their diet depends on the availability of prey in their habitats. Raptors that prey on a wide diversity of species from different taxonomic groups that behave significantly different are termed as dietary generalists. This group usually

includes species that spend more time searching than pursuing prey. Raptors that have a less diverse diet are considered dietary specialists (Steenhof and Kochert 1988; Jimenez and Jaksic 1989; Berkelman 1997; Iriarte et al. 1990; Oro and Tella 1995).

Raptors with a highly specialized diet employ less diverse hunting strategies, however species with a narrow food-niche will shift their prey preferences in seasons of food shortage, particularly in areas were environmental conditions change greatly or as a consequence of changes in prey distribution, abundance and detectability. Morphological specialization for the capture and consumption of particular prey reduce raptors efficiency for feeding on alternative foods and this is reflected in a less diversified diet (Benkman 1988; Beissinger 1990; Nystrom et al. 2005; Takeuchi et al. 2006).

Hunting by a bird of prey can be divided in two parts: the search and the attack. Search strategies most commonly used include still-hunting, fast contour-hugging flight, high searching, stalking and listening. Most common attack strategies include direct and indirect flight attack, tail chase, glide attack and drops or stoops (Fox 1995).

Still-hunting is considered to have low energetic cost. This method is usually performed by birds perching in advantage points where they wait until a suitable prey is spotted (Toland 1987). In fast contour-hugging flight, the raptor flies rapidly and close to the ground, forests canopy or along edges to take flushed prey (Fox 1995). Energetically, fast-contour hugging and tail chases are considered four times more costly than still hunting from perches (Toland 1987).

Soaring is widely used by raptor species with low wing load to locate food either by sight or smell. Raptors soar at low or high altitude gaining lift from rising wind currents or thermals. When foraging, new and old world vultures and certain eagles and hawks climb by circling in a thermal and then glide down slowly looking for food. Other species, particularly falcons soar to gain altitude and then attack their prey by descending abruptly in long, fast and sometimes vertical stoops (Pennycuick 1973; Cade 1982; Houston 1986). Other hunting strategies include group or cooperative hunting (Mader 1978) and many species will stalk prey, particularly when invertebrate prey is abundant (Willis et al. 1983; Thorstrom et al. 2000).

1.8 Diet

Birds of prey are at the top of the food chains (although not completely free of predation), and as such, are considered good models for studies on the structure and niche attributes in a predator community, on the relationships between predators within a guild, and on responses of predators to variations on prey abundance (Jaksic 1985; Nystrom et al. 2005). Additionally, studies on raptors´ diet can provide data on the ecology of species and their prey and may help to understand the make-up and structure of communities (Bonvicino and Bezerra 2003; Marti et al. 2007).

Early methods for the study of raptors diet were based on the examination of stomach contents during collection of museum specimens. Today, methods are less invasive and include direct observations of hunting individuals and prey deliveries at nesting sites, collection and analysis of pellets and prey remains

under feeding perches, inside nests and under nesting sites (Hector 1985; Robinson 1994; Nielsen 1999). These methods are not only used to characterize prey diversity but also biomass of prey consumed which helps to determine the importance of particular prey species in raptor diets during certain periods of their life history (Oro and Tella 1995; Takeuchi et al. 2006).

Given the low density of raptor species and their difficulty in detection, direct observations of successful hunting attempts are sporadic and identification of preys carried or consumed at feeding perches difficult. For these, most studies on raptors diet have been conducted around nesting sites diet composition is usually restricted to prey items consumed during their breeding cycles and might not reflect species prey preferences during their entire life history (Klein et al. 1988; Robinson 1994; Piana 2007).

1.9 Breeding

Knowledge of the breeding behavior and requirements of raptors species is considered a key factor for their conservation, however basic information on the breeding of several species, particularly those inhabiting tropical forests is still incomplete and even nonexistent (Bierregard 1998).

Most of the Falconiformes, and particularly the Accipitridae, built nests but some will lay eggs inside abandoned cavities in trees and rock ledges, abandoned nests and even on the ground. Clutch size varies from one to several eggs per breeding cycle and development before fledging can take some weeks in smaller species (*Accipiter spp.*) to six months in the larger ones (i.e. Harpy Eagle –*Harpia harpyja*). Nest predation, food shortage and siblicide are

considered the main causes of low nesting success and productivity in birds of prey (Meyburg 1973; Sibley 2001). Species with low reproduction rate and productivity are considered more susceptible to extinction (Terborg 1974; Kruger and Radford 2008).

Breeding of raptor species, behavior of parents and their role during breeding (nest attendance, parental roles, etc.), breeding success, clutch size, nest productivity, chick development, fledging and dispersal is usually documented by means of direct observations of wild individuals at nests. This information, when combined with demography parameters is fundamental to assess response of species to habitat destruction (Berkelman 1996; Bierregard 1998; Delannoy and Cruz 1988).

1.10 Communities

As in other terrestrial taxonomic groups, raptor communities have an increasing number of species from the poles to the equator and in general, warmer climates result in a greater diversity of species. This is probably a result of the increased proportions of forested areas, rainfall and mountain ranges existing in the tropical regions of the world (Newton 1979; Rohde 1992; Fuchs et al. 2011).

Partitioning of limited biotic and abiotic resources contributes to the coexistence of species within complex assemblages while specialization along some resource dimensions may segregate species and individuals within them (Schoener 1974; Schoener 1984; Solonen 1994; Katzner et al. 2003). The structure of raptor communities is a result of the occurrence of species and their abundance which in turn are a consequence of their habitat requirements and

distribution, diet preferences and morphology (Jaksic 1982; Simmons 1985; Thiollay 1993; Solonen 1994; Petty et al. 2003).

Given that raptors are suspected to forage in habitats were calorific intake is higher, food availability is suspected to be a very important factor contributing to raptor diversity and abundance. This is mostly because prey acts as a limiting factor on reproduction, influences the use of space and affects the composition of communities at least on a temporal basis (Smith et al. 1981; Steenhof and Korchert 1988; Korpimaki and Nordahl 1991; Solonen 1994; Buchanan 1996; Rohner 1996; Marzluff et al. 1997; Krueger et al. 2002).

Habitat diversity, vegetation structure and topography also affect the composition of raptor communities and play a key role in raptor assemblages (Janes 1985; Preston 1990; Wightman and Fuller 2005). In southern India, raptor diversity increased from open areas to closed forest, but the highest number of species occurred at edges and woodlots were species of all habitats tended to merge. In French Guiana raptors were more diverse in areas with greater habitat diversity (Thiollay 1993 and 2007). Changes in forest cover affects prey detection and availability influencing the abundance of raptor species in a given area (Tjenberg 1985; Pedrini and Sergio 2001; Whitfield et al. 2007). Availability of nesting sites, which is often related to habitat characteristics, also acts as driving force in shaping raptorial communities (Solonen 1994; Katzner et al. 2003).

1.11 Demography

A main goal of raptor demography studies is to obtain numbers of species abundance to make inferences about population status, habitat associations and population trends which can then be used to foster species conservation (Norvell et al. 2003; Andersen 2007). Despite being a particular difficult group to survey, researchers have spent a lot of time and effort to count raptors to estimate population size, monitor populations of conservation concern and even compare different methods for counting them (Fuller and Mosher 1985).

Different research techniques used to obtain data on raptors´ demography include point and transect counts, spot-mapping, and capture and marking of individuals (Fuller and Mosher 1985; Thiollay 2007). Distance sampling, a group of method used to estimate the absolute density and abundance of biological populations have been extensively used in several bird (and other) taxa yet its use in Falconiformes is still scarce (Andersen et al. 1985; Marsden 1999; Boano and Toffoli 2002; Lloyd 2003). This could be attributed to the relatively high number of records per species (between 40 and 100) needed to confidently estimate species densities. However, an advantage of Distance sampling over other methods is that densities obtained are not affected by different detectability of species (Rosenstock et al. 2002; Thomas et al. 2002).

Raptor counts along roads, a variation of transect counts have become very popular to obtain indices of raptors relative abundance (Fuller and Mosher 1985; Ellis et al. 1990; Jensen et al. 2005). However, when using this method, researchers need to be aware that important sources of variation in species detectability caused by vegetation or habitat structure, by the behavior or size of the target species or by different observers will affect counts. These sources of

bias must be taken into account during study design and data analysis. Perhaps most importantly, researchers should be aware that values of relative abundance do not have a known relationship to true density, so demography data derived from abundance indexes should be interpreted with care (Millsap and LeFranc 1998, Rosenstock et al. 2002; Norvell et al. 2003).

1.12 Raptor conservation and threats

Among the Accipitridae, nine species are listed as critically endangered, eight as endangered and 26 as vulnerable. These species include vultures from tropical Asia that are affected by indirect drug poisoning, and species endemic to tropical islands and forests that are seriously affected by habitat destruction and direct prosecution (BirdLife International 1992, Mañosa et al. 2003; BirdLife International 2008; Remsen et al. 2011). Among the Falconidae, five species are threatened by habitat destruction, prosecution, and illegal traffic. The critically endangered California Condor (*Gymnogyps californiacus*: Cathartidae), is the only threatened species within its family. The species suffered serious declines due to prosecution and indirect lead poisoning (BirdLife International 1992 and 2008).

Habitat loss is considered the main threat to raptors and this is the main cause of population decline for most species listed as threatened by BirdLife International (2008). This is particularly alarming in highly diverse ecosystems and islands in the tropics where destruction, disturbance and fragmentation of forests continues and will persist if increased conservation efforts are not implemented (Thiollay 1994; Myers et al. 2000).

Human population growth is one of the major drivers affecting raptors because as population increases the loss of primary and native habitats caused by urbanization and development also increases (Thiollay and Rahman 2002; Carrete et al. 2009). In urban areas raptor diversity is reduced and assemblages are less complex particularly where human induced impacts are more severe due to habitat reduction and urban encroachment (Jaksic et al. 2001; Thiollay and Rahman 2002).

Important habitats for raptor species such as tropical forests and plains are continuously lost by the removal of vegetation cover for agriculture while wetlands are drained and turned into crop plantations. In Africa, raptor diversity has been severely reduced outside protected areas as natural habitats are transformed for agriculture and cattle grazing (Seavy and Apodaca 2002; Thiollay 2006b). Additionally, deserts and dry savannas are lost as irrigations give way to agricultural fields. Conversion of open country to cattle grazing and monocultures also have detrimental effects in raptor populations not only because the vast expanses of habitat and prey species that are lost but also because the use of pesticides (Bierregard 1988; Mooney 1998; Sorley and Andersen 1994).

In forested ecosystems timber extraction can negatively affect raptors abundance, nest availability and reoccupancy and can cause nestling mortality (Penteriani and Faivre 2001; Vargas et al. 2006). Subsistence and commercial hunting in natural environments can deprive raptor species of favored prey and human activities around active nests affect hatching rates reducing nest productivity in large species. Additionally, direct prosecution (shooting and poisoning) of raptors has depleted populations in urban and rural areas

worldwide (Kenward 1999; Whitfield et al. 2004; Gonzales et al. 2006; Vargas et al. 2006).

Indirect poisoning of birds of prey has become a serious factor affecting their populations. This is particularly relevant in Old World vultures feeding on carcasses of livestock treated with the drug diclofenac which has lead to serious declines in populations of at least four vulture species that are now critically endangered (Oaks et al. 2004; BirdLife International 2008). Poisoning of raptors due to the ingestion of lead ammunition (and other toxics) found in carcasses is known to affect California Condor populations and those of other scavenging species (Henny and Elliot 2007).

Although not as relevant as direct prosecution, electrocution of raptors that perch on transmission poles or collide with power lines is increasing as a result of the expansion of electric lines associated with rapid urbanization in rural areas (Xirouchakis 2004; Alvarado and Roa 2011). Construction of wind farms across the world has increased the risk of birds colliding with rotor blades, although this still infrequent (Hunt 2000; Thelander and Rugge 2000; de Lucas et al. 2004; Drewitt and Langston 2006). Data on raptor mortality caused by wind turbines is still scarce and the methodology to measure it has not been standardized. As the demand for alternative fuel sources across the globe increases, more research is needed to fully assess the impacts of wind farms on raptors (Drewitt and Langston 2006; Madders and Whitfield 2006).

Trapping of wild birds and the collection of eggs from active nests for the sport of falconry has been a cause for the decline of a number of raptor species, particularly of Saker (*Falco cherrug*) and Peregrine (*Falco peregrinus*) falcons in

Asia and Europe. However, in recent years an increased use of captive bred falcon and hybrids, particularly in the Middle East has reduced the demand for trapped birds (Barton 2000). The legal framework for falconry worldwide regulates and enforces the sustainable and humane use of wild and captive bred raptors for falconry and many falconers are involved in research and conservation of raptors worldwide. It was a result of research conducted by North American falconers through breeding and release of juvenile peregrines that the species recovered after being severely affected by contamination from DDT and related pesticides in the late 60´s and early 70's (Hickey and Anderson 1968; Bond 2007).

1.13 Raptors in Peru

Despite being one of the most raptor diverse countries in the world, little is known about the Falconiformes in Peru. Only four studies on the structure of Peruvian raptor communities have been published: Two were conducted in the Amazonian lowlands of Madre de Dios (Robinson 1994; Valdez 1999), one in the forests of northwest Peru (Piana and Marsden 2012) and one in the dessert plains in the northwest (but only included the guild of carrion feeders) (Wallace and Temple 1987). The distribution of raptor species throughout the country is continuously being updated as more bird surveys are conducted in remote regions (Piana et al. 2010; Angulo and Piana 2011).

In Peru, ten raptor species are threatened. The endangered Andean Condor is protected by Peruvian law and was widely persecuted in the past to protect sea bird colonies nesting on guano islands. Today, direct persecution of Andean

Condors in coastal ecosystems has ceased but young and adult individuals are still captured and used in traditional ceremonies (Yawar Fiesta) in some Andean towns. Although birds are released after the ceremonies, it is suspected that the survival rate of these birds is low (McGahan 1971). Research is urgently needed to measure the impact of Yawar Fiesta in Andean Condors within the Peruvian Andes.

Destruction of montane ecosystems east of the Andes for agriculture and grazing is probably the main threat for one endangered species (Solitary Eagle –*Harpyhaliaetus solitarius*) and three vulnerable species: The Semi-collared Hawk (*Accipiter collaris*), the Black-and-Chestnut Eagle (*Spizaetus isidori*) and the Barred Hawk (*Leucopternis princeps*) (BirdLife International 2012). With populations restricted to mangrove forest in Tumbes, habitat destruction is also suspected to be the main threat for Mangrove Hawks (*Buteogallus subtillis*) in Peru (BirdLife International 2012).

The Harpy and Crested Eagle (*Morphnus guianensis*), are two vulnerable species from the eastern lowlands that are threatened by destruction of forests as road construction and timber extraction increases throughout its range. Adult and young individuals of these species are continuosly killed as trees supporting active nests are logged and individuals are hunted for food or souvenirs (Piana 2009).

The endangered Gray-backed Hawk (*Leucopternis occidentalis*) is a Tumbesian endemic occurring in western Ecuador and extreme northwest Peru. In Ecuador its population is in constant decline due to severe habitat loss for agriculture and grazing. In Peru data on the species demography has not been published

and its distribution is still unknown. This information is urgently needed to assess it's status globally and implement conservation measures to protect this species along its entire range (Vargas 1995; BirdLife International 2008).

1.14 Aims of the PhD and overview and aims of chapters

This PhD examines those factors that contribute to the makeup of the raptor community that inhabits the forests of the North West Biosphere Reserve (NWBR) in extreme northwest Peru. It focuses on finding those parameters (geographic and floristic) that influence the distribution of species in the landscape. It makes a revision of the current methods used to estimate raptor densities and uses a Distance Sampling method to estimate absolute density and population sizes of raptors in the study area. This PhD also measures the impact of cattle grazing on raptor species distribution, by estimating cattle density through dung counts.

The aims of the PhD are:

- To determine the ecological factors that influence the occurrence, distribution and abundance of diurnal raptor species in northwest Peru and to use these data to predict future responses of key species to environmental change.
- To improve the methods used to estimate demographic parameters in the Falconiformes and to use novel variants of Distance sampling transect methods to assess population sizes and densities of raptor species.

- For a number of species occurring in the study area, predict how human induced habitat alterations will affect them individually and to the assemblage as a whole.
- To use information obtained from data analysis to generate management recommendations that promote raptor conservation in the NWBR and in extreme northwest Peru.

Chapter 2: *Tropical dry forests, study area and field methods*

Overview: In this chapter I review the distribution of dry forest in the world and Peru, describe the characteristics of the study area and provide details on the field methods used to measure habitat parameters and raptor along transects. More methodological details are given, together with statistical analysis in the following four data chapters.

The aims of this chapter are:

- To assess the distribution and level of threat of tropical dry forests worldwide and in Peru.
- To describe the study area, its different habitats and their relationship to different areas of endemism and biomes occurring in South America.
- To describe the different and more general field methods used during field work to collect data on the distribution of raptor species and those used to measure habitat variables.

Chapter 3: *Diversity, community structure and niche characteristics within a diurnal raptor assemblage of northwest Peru*

Overview: I explore how diversity and abundance of raptors is related to habitats types and land uses and asses those factors that drive raptor community make up in the study area. Species realized niches characteristics that can be used for habitat management and ultimately for species conservation are also discussed.

The aims of this chapter are:

- To measure niche width, niche position, niche bottlenecks, and spatial niche overlap within raptor community and to assess the influence of these parameters in shaping the structure of the raptor community in northwest Peru.
- To identify environmental and geographical variables that promote or constrain raptor species presence in the study area and that segregate and/or aggregate them along different niche dimensions.
- To use niche characteristics within species to identify those of conservation priority.

Chapter 4: *Habitat associations within a raptor community in a protected area in northwest Peru*

Overview: Environmental data collected along transects is used to obtain habitat models for raptor species and to identify combination of habitat parameters (floristic and geographic) that best predict species presence. These

results are further discussed in relation to habitat management strategies that are needed to maintain species of conservation concern in the NWBR, and buffer areas in extreme northwest Peru.

The aims of this chapter are:

- To identify environmental and geographical variables that are likely to be more relevant in influencing raptor species distribution in the NWBR.
- To use logistic regressions to generate habitat models that explain the presence of raptor species within the study area.
- To use these models to identify management interventions or priority areas in order to promote conservation of raptor species in northwest Peru.

Chapter 5: *Densities and population sizes for raptors in a protected area in northwest Peru: Use of Distance Sampling and a review of survey methodologies*

Overview: I review methods most commonly used to estimate demographic parameters of raptors species and explore the pertinence of using a line-transect Distance sampling method to estimate absolute density of raptors. I also explore the influence of time of day and habitat types in species density and explore the use of cluster analysis combined with Distance sampling to estimate absolute densities of rare or less detected species.

The aims of this chapter are:

- To discuss different methods used to estimate absolute density of raptor species.
- To use of Distance Sampling methods along transects to obtain density estimates and population size of raptor species occurring in the study area.
- To obtain density and population size of species in different habitats by using habitat types as a covariate in Multicovariate Distance Sampling (MCDS).
- To improve density estimates of rare species by using statistical hierarchical analysis to group species with similar detection characteristics.

Chapter 6: *Influence of cattle grazing intensity on raptor distribution within a Peruvian protected area*

Overview: Cattle densities derived from dung counts along transects and measured vegetation parameters were used to generate generalized additive models that measured the response of raptor species to increased cattle density in the study area. These data is used to generate cattle management and raptor species conservation recommendations within the NWBR.

The aims of this chapter are:

- To use dung counts to obtain cattle densities in the study area and to relate these to the diversity, abundance and distribution of raptor species.

- To measure the impact of cattle density on the structure of the raptor community and on the distribution of single species in the study area.
- To obtain threshold levels of cattle density that can be used as gross management tools to maintain the highly diverse community of raptors that is characteristic of northwest Peru.

Chapter 7: *Discussion: Conservation priorities, management recommendations and the future of raptor research*

Overview: I point out at the importance of raptor conservation, review the most relevant findings of this thesis and discuss the implications of habitat fragmentation within the Tumbesian Centre of Endemism. Then I define priorities for habitat management and raptor research in the NWBR and the tropical regions of the world while point at future research directions for estimating demographic parameters of tropical raptor species.

The aims of this chapter are:

- To highlight the importance of raptor conservation worldwide and within neotropical ecosystems in particular.
- To promote habitat connectivity within the Tumbesian Endemic Centre (and elsewhere) for species conservation, particularly those that are endemic or threatened.
- To provide recommendations for the management of cattle grazing within the NWBR.

- To highlight the great potential of distance sampling methodology to obtain demographic parameters of raptor species worldwide, but particularly in areas similar to those found in extreme northwest Peru.

Chapter 2: Tropical dry forests, study area and field methods

2.1 Tropical dry forests

Tropical dry forests have been considered as the most endangered of all remaining habitat types (Janzen 1988), and although present in all the tropical portions of the world, approximately 54% of remaining tropical dry forests are located in South America (Miles et al. 2006). Throughout their range, these forests are subject to a wide variety of threats mainly as a result of human activities. Forest fragmentation, burning, and conversion for agriculture and pasturelands, are perhaps the most important of these threats (Miles et al. 2006).

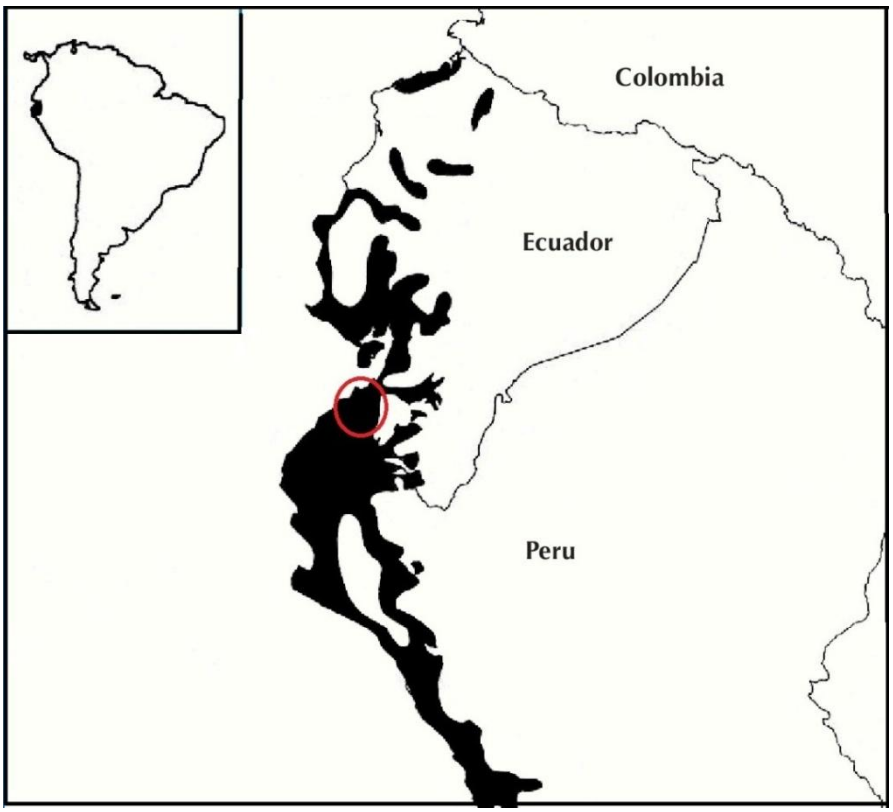
2.2 The Tumbesian Centre of Endemism in Peru

In Peru three main tropical dry forest types occur: i)The inter Andean seasonally dry forests, mainly located within the Marañon and Mantaro river basins in the northern and south-central portion of the Andes, ii) the eastern seasonally dry forest in the San Martín department northeast of the Andes, iii) the equatorial seasonally dry tropical forest of northwest Peru (from Tumbes to the northern portion of La Libertad department) that overlaps with the Tumbesian Centre of Endemism (Linares-Palomino 2004 and 2006).

Located south of the Chocó Endemic Area and west of the Marañon Endemic Area, the Tumbesian Centre of Endemism (sensu Cracraft 1985) or the Tumbesian Endemic Zone is considered of high conservation priority (Myers et al. 2000; Figure 1). With 55 bird species restricted to this region, the Tumbesian

Centre of Endemism has one of the highest numbers of endemic bird species among all the endemic bird areas of South America. Of these, 16 species are threatened, with habitat loss and alteration as the main cause of threat (Best and Kessler 1995).

Figure 1: Map of the Tumbesian Centre of Endemism (adapted from Best and Kessler 1995) and detail of study area (in the circle).



2.3 Protected areas in extreme northwest Peru

Located within the equatorial seasonally dry forest in extreme northwest Peru, and in the centre of the Tumbesian Centre of Endemism, the North West Biosphere Reserve (NWBR) is a set of three adjacent protected areas (the Cerros de Amotape National Park –CANP, the Tumbes National Reserve –

TNR, and El Angolo Hunting Preserve -EAHP) that together preserve 230,000 hectares of dry, semi-deciduous and deciduous forests. These three protected areas are Important Bird Areas (IBA) and they form the largest tract of these forest types still remaining in the whole Tumbesian Centre of Endemism (Best and Kessler 1995; Angulo 2009).

With 36 species so far recorded, and despite being a predominantly arid region, raptor diversity in the Tumbesian Centre of Endemism in Peru is unusually high (Piana 2011). This high diversity is presumably related to the overlap and close proximity of four biomes and several endemic bird areas (Best and Kessler 1995). Additionally, the Porculla Pass (2,150 m asl.), the lowest pass along the entire tropical range of the Andes, lies within this region and might have allowed some species to cross from the eastern lowlands to the eastern side of the Andes and vice versa. Also, the continuity of forested ecosystems west and north of the Andes might have promoted migration of species from central America and colonization further south (Best and Kessler 1995; Stotz et al. 1996; Birdlife International and Conservation International 2005; Fuchs et al. 2011).

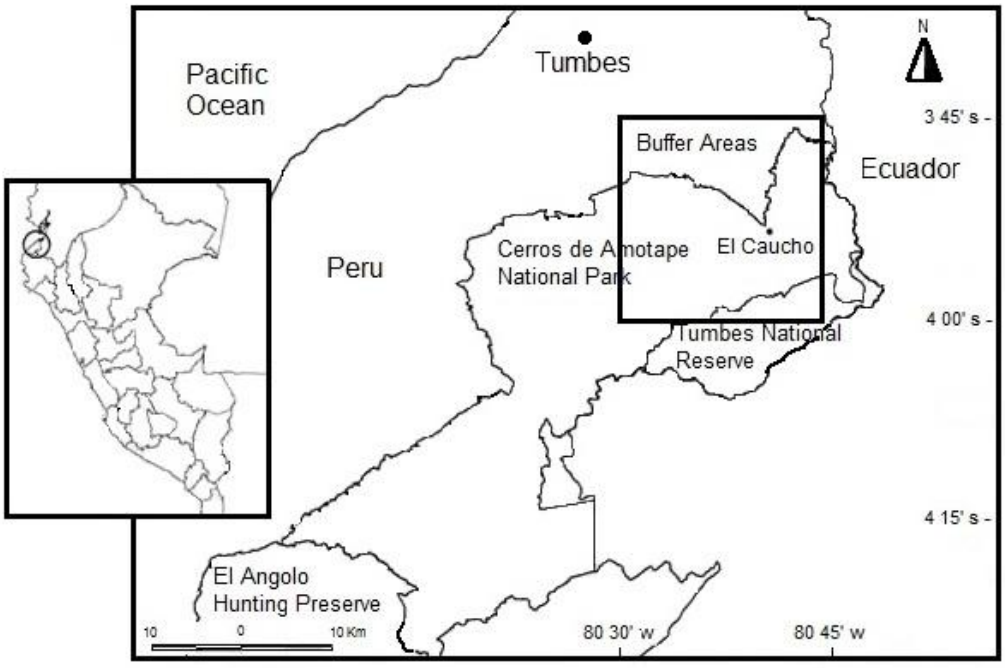
Figure 2: Human activities in the study area (from left top corner and clockwise) include fuel wood extraction, forest clearing for agriculture, timber extraction and free-range cattle grazing.

Figure 3: Cattle grazing and its impact in the Tumbes National Reserve (TNR).

2.4 Study area

I selected a study area of 25 x 25 km (62 500 ha) in the northern part of the NWBR; the centre of this square lying approximately over the El Caucho Research Station. The study area encompassed the northern sector of the CANP and the TNR: From the small town of El Tutumo (3º45´S) in the park´s buffer area to Quebrada El Ebano (4º S); and from the small town of Belen (80º30´ W) to the Tumbes River on the border with Ecuador (80º45´ W -eastern limit of the TNR; Figure 4). With an altitude of up to 900 m asl, topography is mainly influenced by the Cerros de Amotape Cordillera which runs southwest to northeast from the study area.

Figure 4: Study area showing the three protected areas that form the North West Biosphere Reserve and location within Peru.



Precipitation in the study area is approximately 900 mm per year and is markedly seasonal with a rainy season from January to March (90% of annual precipitation) (Nunez and Zegarra 2006). Average yearly temperature is 26ºC, with temperatures higher in lower areas. During El Niño Southern Oscillation (ENSO) events, precipitation in Tumbes department can be many times higher than in average years, while average temperature can increase by 2ºC (CDC-UNALM 1992). During ENSO periods, sea-surface temperatures increase as warm sea currents from the north displace the cold waters of the Humboldt Current. Water vapour in the air increases as water temperature rises. This then precipitate as warmer air coming from the sea ascends through the western ranges of the Andes. Drastic changes in vegetation cover and structure can occur over short periods of time in the study area, particularly during and after ENSO events (Linares-Palomino 2005).

The study area includes four main habitat types within the equatorial seasonally dry tropical forests of northwest Peru (Linares-Palomino 2006). Classification of these habitats is based on Aguirre et al. (2006) although I further divided the deciduous forest into two habitat types. The habitats considered were: Dry savanna (between 30 to 100 m asl) where Algarrobo (*Prosopis pallida*) and Faique (*Acacia macracantha*) trees dominated the vegetation; dry deciduous forest (100-300 m) where Madero (*Tabebuia bilbergi*) trees dominated and with presence of Ceibo (*Ceiba trichistrandra*) and Pasallo *(Eriotheca ruizii*) trees; deciduous forest (300-600 m) where Guasimo (*Guazuma ulmifolia*) dominated the lower strata and Ceibo the upper strata, and semi deciduous forest (> 600 m) with presence of Fernán Sanchez (*Triplaris cumingiana*), Guaruma (*Cecropia litoralis)*, Polopolo (*Choclospermun vitifolium*) and Ceibo (Figure 5).

CANP is a strictly protected area where no direct use of natural resources is permitted. However, due to poorly implemented control policies the park is used for free-range cattle grazing and hunting (Piana pers. obs). TNR is a national protected area where direct use of natural resources is allowed as long as these are compatible with the objectives of the reserve and its management plans. In the sections I surveyed, these activities included low-to-moderate intensity timber extraction, hunting, cattle grazing and conversion of forest to pastures (Figures 2 and 3). According to the Peruvian Law No. 26834, buffer areas are not part of the protected areas yet activities conducted here should be compatible with the objectives of the protected areas adjacent to them. Despite this, human induced activities in buffer areas in the study site ranged from forest clearing for agriculture and cattle grazing, free-range cattle grazing, hunting, commercial and subsistence timber extraction, non-timber forest product extraction (e.g. collection of fruits, parrots, etc.). During field work I never encountered any representatives of the park or reserve administration in the buffer areas.

Figure 5: Habitat types in the study area (from left top corner and clockwise):Dry savanna, dry deciduous forest, deciduous forest and semi deciduous forest.

2.5 Field methods

2.5.1 Raptor surveys and habitat recordings

Data on raptors and associated habitat measures were collected during two field seasons April-December 2008 and April-December 2009. Such long periods in the field were necessary to cover large areas and to accumulate sufficient raptor records. Long field seasons may introduce biases due to seasonality, but I surveyed only outside of the local wet season. All raptor species included in surveys were resident in the area. Evidence suggests that in habitats similar to mine, breeding is most likely during the wet season (Vargas 1995) and no transportation of nesting materials, active nests, or prey supply to nestlings was recorded during the fieldwork.

Seventy (70) one-km^2 plots (1 x 1 km) were positioned in the 25 x 25 km study area (11.2% of the total area). Plots were allocated randomly without stratification within all areas of the study site except the TNR. I positioned six plots inside the TNR because I wanted to measure the impact of intensive cattle grazing on the raptor community. A small number of plots were too remote to allow safe access, so plots up to 2 km closer to existing trails were substituted for these (Thiollay 1993). No two plots were chosen if they fell in adjacent squares. I used existing trails as transects or cut new ones; transect length was 1.8 km in each square, and were ideally 0.7 km long, followed by a stretch of length 0.4 km perpendicular to the first stretch, and finally another stretch of 0.7 km parallel with the first. Walking speed was maintained at 1 km h^{-1}. Speed was maintained by constantly monitoring the time spent walking and distance traversed with a GPS.

Seventy transects were walked in the morning, 90 min after sunrise (approximately 6.30 AM) or sometimes later if rainy or foggy conditions reduced raptor detectability/activity (Thiollay 1989). Additionally, to increase sample size and to measure the effect of time of day in raptor abundance, I evaluated 36 plots from 3.00 PM to 5.00 PM. I accept that time spent surveying within km squares was low (around two hours on the formal survey). This may give rise to problems with defining true absences from squares, especially if raptors were more easily detected in some habitats than others (Buckland et al. 2001).

All diurnal raptors along each transect were recorded and notes were taken to register whether individuals were flying, perched, seen or heard upon detection (Boano and Toffoli 2002). Birds were identified to species and age. The horizontal distance to each encounter was recorded using a laser range finder (Andersen et al. 1985; Rosenstock et al. 2002). For birds that were soaring in circles above the forest canopy, I calculated the centre of these circles during displays or soaring flights and then measured the distance from this point to the transect with a laser range finder. Additionally characteristics of individuals were recorded (absence of feathers due to moulting on flying birds) and birds that were suspected to have been previously detected were excluded from the counts. I acknowledge, that some degree of double-counting of individuals may have occurred; yet double counting is generally of little consequence if such events are relatively infrequent as in my research. Additionally, only one transect was surveyed on a given day and transects were separated more than one kilometre form each other, thus minimizing the

chances of counting the same bird in two different transects (Buckland et al. 1993; Rosenstock et al. 2002).

Species included in these analyses were Turkey Vulture (*Cathartes aura*), Black Vulture (*Coragyps atratus*), King Vulture (*Sarcoramphus papa*), Bicolored Hawk (*Accipiter bicolor*), Crane Hawk (*Geranospiza caerulescens*), Great Black Hawk (*Buteogallus urubitinga*), Harris´s Hawk (*Parabuteo unicinctus*), Gray-backed Hawk (*Leucopternis occidentalis*), Short-tailed Hawk (*Buteo brachyurus*), Zone-tailed Hawk (*Buteo albonotatus*), Savanna Hawk (*Buteogallus meridionalis*) Black Hawk Eagle (*Spizaetus tyrannus*), Laughing Falcon (*Herpethoteres cachinnans*), Crested Caracara (*Caracara cheriway*) and Bat Falcon (*Falco rufigularis*) (Figures 6 and 7).

2.5.2 *Habitat evaluations*

Habitat measurements were taken at eight points, 200 m apart, along each transect (i.e. eight points per sq km). To avoid possible biases derived from sampling along edges, evaluations were conducted 15 m perpendicular to the trail inside the forest. Elevation, latitude and longitude were recorded with a GPS, and gradient was measured with a clinometer at each point along the transect. Although the study area is not large, geographical coordinates are seen as being important as they allow identification of geographical relationships within the raptor community (for example the north tends to be wetter than the south). There was no significant correlation between elevation and latitude or longitude (r_{sMax} = 0.12, P_{Min} = 0.33) so the geographical variables are not simply surrogates for relief.

Canopy height and height of upper vegetation strata (the height at which the mid point of the uppermost vegetation continuum was located) were visually estimated, and percentage cover at different four vegetation strata (0-1 m, 1-5 m, 5-15 m, and 15-25 m above ground) was estimated. These vegetation covers were estimated by eye in increments of 5% within a 10 m radius circle above the recorder. They were then averaged across the eight points along each transect, to some degree lessening issues of inaccuracy or unusual readings at individual points. The two largest trees within a 15 m radius of the plot's central point were selected, and identified to species if they belonged to one of the following tree species: Algarrobo, Faique, Madero, Ceibo, Guasimo, or Polopolo (see Study area section for details of these trees' ecological significance). The diameter at breast height (DBH) of these two trees was measured (Marsden and Whiffin 2003; Lloyd 2008).

Figure 6: Raptors in the study area (from top left corner and clockwise) Turkey Vulture, Black Vulture, King Vulture, Great Black Hawk (immature), Savanna Hawk and Harris's Hawk (immature).

Figure 7: Raptors in the study area (from top left corner and clockwise) Gray-backed Hawk, Short-tailed Hawk, Black Hawk-Eagle (immature), Laughing Falcon, Crested Caracara and Bat Falcon.

Chapter 3: Diversity, community structure and niche characteristics within a diurnal raptor assemblage of northwest Peru

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3.1 Abstract

Despite high raptor diversity and species of conservation importance, little is known about the structuring of raptor communities in tropical regions. I examined diversity across land uses, spatial niche overlap among species, community structure, and relationships between abundance and niche position/width within a diurnal raptor assemblage in Peru. Between April and December in 2008 and 2009, raptors were surveyed using a distance sampling transect method, and associated habitat data collected, in 70 randomly selected one square kilometer plots in Cerros de Amotape National Park, the Tumbes National Reserve and its buffer areas. A total of 563 individual sightings of 19 diurnal raptor species were recorded. Abundance and richness were highest in the buffer zone and lowest in the national park. Mantel tests revealed no correlation between spatial niche overlap between species and body size differences, but there was a near-significant relationship between spatial niche overlap and dietary overlap. A Canonical Correspondence Analysis (CCA) of raptor species and habitat variables ordinated species according to latitude, elevation, percentages of vegetation cover, and, in some cases, individual tree species. Abundance was negatively correlated with habitat niche position (rarer species used 'more extreme' habitats) and positively correlated with niche width (standard deviations of CCA axis scores). There was, however, considerable variation in the abundance-niche width

relationship, and I was able to identify species with narrower-than-expected niches. I then calculated ‘niche bottlenecks’ for each species. There was a strong negative relationship between degree of bottleneck and abundance, with the small rare species having particularly narrow bottlenecks.

3.2 Introduction

Tropical ecosystems are the most diverse in the world (Wilson 1988), with 90% of all raptor species occurring wholly or partially in the tropics (Kennedy 1986). With around 36 species, the forests of extreme northwest Peru hold a particularly rich assemblage of raptor species (Piana et al. 2010) including the endangered Gray-backed Hawk (*Leucopternis occidentalis*). Thiollay (1994) considered this region as a priority area for raptor conservation based on the high diversity of raptor species and the occurrence of several endemics. As elsewhere in South America, the drier forests of Tumbes are particularly threatened - in western Ecuador and northwest Peru less than 5% of forest cover remains (Best and Kessler 1995).

Birds or prey are difficult to study, the status and distribution of many species remain poorly known (Bildstein et al. 1998). As top predators, raptors usually occur at low density and occupy large territories, and therefore may be sensitive to habitat degradation (Bierregard 1998, Watson 1998). Thiollay (1998) considered habitat loss, degradation and fragmentation as the main issues in raptor conservation in tropical Asia.

Although several studies have been conducted on tropical raptors, these have concentrated on the abundance, habitat associations and ecology of individual species (Whitacre and Thorstrom 1992) with relatively few attempts to describe raptor community composition (Thiollay 1996, Thiollay 2007, Carrete et al. 2009). Studies attempting to identify factors that segregate sympatric raptor species have generally been oriented towards dietary structuring of communities (Iriarte et al. 1990) although there is evidence that vegetation cover and structure (Preston 1990), availability of nesting and perching sites are also factors that segregate (or aggregate) raptor species in the landscape (Janes 1985).

Few attempts have been made to characterise and compare habitat niche dimensions such as niche position, width and overlap across raptor species (an exception is Thiollay 1993). In this chapter, I deal with the ideas of the Grinnellian or Hutchinsonian niche (the habitats within which a species is found, or the multi-dimensional 'hypervolume' within which it is found) rather than the Eltonian niche (how a species fits into a community). Niche position can be defined as the typicality of the conditions used by a species (Gregory and Gaston 2000) and, in this study, reflects how extreme or 'average' are the habitats used by a species relative to those available in the landscape. Niche width can be defined as the range of conditions used by a species (Gregory and Gaston 2000, Marsden and Whiffin 2003), and in this study reflects the proportion of the gradient of variability in a composite of habitat measures that is used by a species. Niche overlap is the degree to which two or more species share niches (Pianka 1974). That is the proportion of all geographical areas,

habitat parameters or resources shared by two taxa. In this study I compare spatial niche overlap, or the proportion of sites in which pairs of raptor species were recorded compared to those used by just one of the pair. These measures are seen as being critical drivers of biotic community make-up (Hofer et al. 2004) and have important implications for conservation biology (Devictor et al. 2010). For example, niche position is usually found to have a strong effect on abundance (Seagle and McCracken 1986, Marsden and Whiffin 2003) with extreme niche positions being associated with low abundance, which is itself associated with high extinction risk (Pimm 1988). Niche width is generally not thought to have strong influence on abundance (Gaston et al. 1997) but more important may be particularly narrow niche widths along certain niche dimensions. For example, if a species has a broad diet and uses a wide range of habitats for foraging, and yet has an extremely specialised breeding habitat (it has a narrow breeding habitat niche) then it may be particularly vulnerable to relatively small anthropogenic habitat changes if they occur on the dimension on which its niche is narrowest. I term this narrow niche a 'niche bottleneck', and in this study it represents the combination of niche attributes along different niche dimensions that might restrict or constrain the presence of raptor species in the study area (Wiegand et al. 2008; Fort et al. 2009). In this chapter, I compare a species' habitat niche width across several habitat gradients to determine how severe any niche bottleneck might be.

My aim was to examine the make-up of the diurnal raptor assemblage in Tumbes, northwestern Peru, in terms of abundance, spatial niche overlap across species, and the main environmental drivers of assemblage patterns. I

then look at the relationships between abundance and niche characteristics to determine if some species may be particularly susceptible to declines or local extinction due to their specialisation in particular habitats, or their intolerance of anthropogenic environmental changes that are underway in the area. I include an investigation into the extent to which individual species' habitat niches might be constricted on particular habitat gradients and whether such niche bottlenecks have an influence on local abundance.

The aims of this chapter are: 1. To measure niche width, niche position, niche bottleneck, and spatial niche overlap within raptor species to assess the influence of niche characteristics in shaping the structure of the raptor community in northwest Peru. 2. To identify environmental and geographical variables that promote or constrain raptor species presence in the study area, and that segregate and/or aggregate them along different niche dimensions. 3. To use niche characteristics within species to identify those of conservation priority.

3.3 Methods

Nineteen species of raptors were detected during morning transect evaluations, but only fourteen were included in the analysis (those species that were present in seven or more plots). Species included were Turkey Vulture (*Cathartes aura*), Black Vulture (*Coragyps atratus*), King Vulture (*Sarcoramphus papa*), Bicolored Hawk (*Accipiter bicolor*), Crane Hawk (*Geranospiza caerulescens*), Gray-backed Hawk (*Leucopternis occidentalis*), Great Black Hawk (*Buteogallus urubitinga*), Harris´s Hawk (*Parabuteo unicinctus*), Short-tailed Hawk (*Buteo brachyurus*), Zone-tailed Hawk (*Buteo albonotatus*), Black Hawk-Eagle

(*Spizaetus tyrannus*), Laughing Falcon (*Herpethoteres cachinnans*), Crested Caracara (*Caracara cheriway*) and Bat Falcon (*Falco rufigularis*). Species not included (all resident in the study area) were Fork-tailed Kite (*Elanoides forficatus*), Savanna Hawk (*Buteogallus meridionalis*), Roadside Hawk (*Buteo magnirostris*), Collared Forest Falcon (*Micrastur semitorquatus*) and American Kestrel (*Falco sparverius*).

3.4 Statistical analysis

Raptor abundance was expressed in two ways. The first was a simple encounter rate of both flying and perched birds expressed as number of individuals of each species recorded in the 1.8 km of transect within each square and then expressed as number of birds per 100 km. The second was an indication of raptor density derived through Distance sampling (Buckland et al. 2001; Buckland et al. 2008) using DISTANCE 6.0 (Thomas et al. 2010). Recommended number of records for reliable density estimates with Distance analysis is around 100 (Buckland et al. 1993; Marsden 1999) so rare species or those with few records are usually left out of analyses.

Some important assumptions are needed for distance sampling methods to work: 1. All birds on the line of the transect are detected with certainty. 2. Birds are detected at their initial position. 3. Distances are measured exactly. 4. The sample plots are representative of the entire survey region (Buckland et al. 2001; Buckland et al. 2008). Data from both perched records and flying records were included in the analysis, to maximize sample size for individual species, so

my derived densities are more than likely overestimates of true bird density (Marsden 1999). However bird movements were independent from the observer and in most cases flying birds were soaring in circles, so they were moving slowly. For this, I was able to measure the distance from the transect to the centre of this circle with a laser range finder. My method does, however, attempt to account for differences in detectability across species and habitats. During surveys I focused on birds that were closer to the transect and distances to these birds were accurately measured with a range finder. I used Conventional Distance Sampling (CDS) of DISTANCE 6.0 to estimate absolute density of species. There was a significant positive correlation between encounter rates and density estimates for species (r = +0.83, df = 12, P < 0.001).

Differences in raptor encounter rates and species richness (number of species recorded within each km^2) were tested across habitat types and land uses using Kruskal-Wallis ANOVAs. Spatial niche overlap between species' occupancy of km^2 was calculated using the symmetric equation formula proposed by Pianka (1973)

$$O_{ij} = \frac{\sum_{i=1}^{n} pij\ pik}{\sqrt{\left(\sum^{n} pij^2\right)\left(\sum^{n} pik^2\right)}}$$

where *pij* and *pik* are the proportions of all records of the j_{th} and k_{th} raptor species within the i_{th} km^2, with values ranging from 0 (no overlap) to 1 (complete overlap); for this I used the number of plots in which a species was recorded.

Relationships between degree of spatial niche overlap between pairs of species and body size differences (Marquez et al. 2005), and dietary overlap between those pairs of species were examined using Mantel tests with the software PAST (Hammer et al. 2001). Dietary overlap data were taken from the Global Raptor Information Network -GRIN (2010) database and was expressed as the number of dietary items (from a list of nine categories: insects; crustacea; fish; amphibians; reptiles; birds; terrestrial mammals; bats; carrion) shared by each pair of raptor species. Significance level was set at 0.05.

I used Canonical Correspondence Analysis (CCA) in PAST (Hammer et al. 2001) to ordinate raptor species along the main community and environmental axes. CCA is an ordination method that incorporates habitat variables into the analysis so the axes of the final ordination are a linear combination of environmental variables and species data (Ter Brack 1986, Henderson and Seaby 2008). In CCA, explanatory variables are represented as vectors pointing to higher values of that variable; their relative lengths are directly proportional to their importance in influencing community structure (Ter Braak 1986, Grand and Cushman 2003). Only those 14 raptor species recorded in more than seven km^2 were included. Environmental variables entered were means of the variables recorded at each habitat plot along each transect (thus were averages within each km^2). Counts of tree species recorded > 49 times were included (species were Ceibo, Polopolo, Guásimo, Algarrobo, Faique, and Madero).

Values of habitat niche position were calculated for each raptor species by summing the absolute deviations of species centroids from the origin on each of the four main CCA axes. Niche widths were obtained from the standard

deviation values of the presence of species in each plot and canonical values for the first four axes (Carnes and Slade 1982) using SPSS 16.0 software (SPSS Inc. 2007). Canonical values per axis were considered as the dependent variable.

3.5 Results

3.5.1 *Raptor abundance/richness and spatial distribution*

A total of 563 individual sightings of 19 raptors species were recorded along transects, but only species with more than seven records (see Methods) were included in subsequent analyses of species abundance, spatial niche overlap, niche position, widths and bottlenecks. The community was dominated by two vultures Turkey Vulture -148 records, Black Vulture -139 records, along with Harris´s Hawk -55 records, Laughing Falcon -44 records, and the endangered Gray-backed Hawk -34 records. In all, these five species contributed 75% of all raptors recorded. Among Accipitridae and Falconidae species, Harris´s Hawk was detected in 32 plots, Laughing Falcon in 30 and Gray-backed Hawk in 17.

Raptor encounter rates and species richness did not differ across the four habitat types (Kruskal-Wallis non-parametric ANOVA), but did differ (both including and excluding vultures) across the three land use regimes: Cerros de Amotape National Park, Tumbes National Reserve and buffer areas. Encounter rates and species richness tended to be highest in the buffer zone and lowest in the national park (Table 1).

Table 1. Raptor encounter rates (median number of raptor individuals encountered km^{-2} with inter-quartile range in parentheses) and species richness (median number of raptor species recorded km^{-2} with inter-quartile range in parentheses) in different habitat types and land uses. Analyses were performed including and excluding the dominant vulture species Turkey Vulture and Black Vulture. *n* = number of sample squares in each habitat type/land use. * *P*<0.05, ** *P*<0.005, ns not significant.

	Vultures included		Vultures excluded	
Habitat type	Encounter rate	Richness	Encounter rate	Richness
Dry savanna *n*=9	9 (4-14)	4 (2-5)	2 (2-4)	2 (1-3)
Dry deciduous *n*=26	6.5 (4-13)	4 (2-5)	3.5 (2-6)	2 (2-4)
Deciduous *n*=17	7 (3-13)	4 (2-6)	4 (2-7)	3 (2-4)
Semi-decid. *n*=18	5 (2-8)	3.5 (2-4)	3 (2-4)	2.5 (1-4)
Difference	H=3.9 ns	H=1.5 ns	H=4.7 ns	H=3.7 ns
Land Use				
National park *n*=32	4.5 (2-9)	3 (2-4)	3 (2-5)	2 (1-4)
National reserve *n*=6	7 (4-12)	4 (2-5)	4 (2-6)	2.5 (1-4)
Buffer zone *n*=32	16.5 (12-27)	6.5 (4-9)	7.5 (4-13)	4.5 (2-7)
Difference	*H*=13.1 **	*H*=9.2 *	*H*=8.3 *	*H*=5.0 ns

Spatial niche overlap between pair of species is presented in Table 2. There was no significant correlation between measures of spatial niche overlap between species and the differences in their body masses (Mantel test; r = +0.04, P = 0.32). There was, however, a near-significant positive correlation between spatial niche overlap and degree of dietary overlap (Mantel test; r = +0.17, P = 0.09).

Table 2. Measures of spatial niche overlap (Pianka 1973) across fourteen abundant raptors species in Tumbes, northeast Peru.

	Black Vulture	King Vulture	Bicolored Hawk	Crane Hawk	Great Black Hawk	Harris's Hawk	Gray-Backed Hawk	Short-tailed Hawk	Zone-tailed Hawk	Black Hawk-Eagle	Laughing Falcon	Crested Caracara	Bat Falcon
Turkey Vulture	0.68	0.20	0.12	0.20	0.34	0.81	0.29	0.38	0.44	0.20	0.30	0.33	0.32
Black Vulture		0.33	0.02	0.10	0.35	0.63	0.30	0.47	0.38	0.28	0.20	0.34	0.26
King Vulture			0.11	0.00	0.33	0.13	0.28	0.20	0.03	0.24	0.24	0.09	0.19
Bicolored Hawk				0.07	0.16	0.18	0.00	0.00	0.07	0.08	0.15	0.00	0.00
Crane Hawk					0.00	0.11	0.14	0.19	0.00	0.10	0.04	0.00	0.00
Great Black Hawk						0.52	0.29	0.42	0.25	0.27	0.19	0.13	0.23

Harris´s Hawk	0.22	0.42	0.27	0.31	0.38	0.60	0.33
Gray-backed Hawk		0.38	0.39	0.26	0.28	0.06	0.42
Short-tailed Hawk			0.34	0.36	0.24	0.20	0.21
Zone-tailed Hawk				0.10	0.36	0.00	0.17
Black Hawk-Eagle					0.25	0.00	0.07
Laughing Falcon						0.05	0.21
Crested Caracara							0.00

3.5.2 *Raptor community and vegetation ordination*

The four most important CCA axes together accounted for 70.4% of overall variation in the raptor and environmental data. Figure 8 shows correlations between individual environmental variables and numbers of key tree species recorded within plots, and scores on axes 1 and 2, and Table 3 provides descriptions of the four main CCA axes. Elevation, latitude, tree sizes (DBH and height), percentage of vegetation cover between 5 to 15 m, and numbers of tree species such as Guasimo and Polopolo were among the most powerful variables to separate raptors species (Figures 8 and 9).

Table 3. Description of the four main axes of CCA.

Axis (eigenvalue)	Strongest correlation	Interpretation
1 (0.25)	Elevation (+), Tree DBH (+), % vegetation cover 5-15 m (+) Latitude (-), and Algarrobo (-)	Increasing altitude with greater prevalence of large, tall trees and fuller mid-level cover in south.
2 (0.15)	Tree DBH (+), Tree Height (+), Guasimo (-), % vegetation cover 0-1m (-).	Large trees with sparse ground cover and absence of Guasimo trees.
3 (0.12)	Latitude (-), % vegetation cover 1-5m (-), Ceibo (+), Elevation (+).	Higher areas south of study site with open low strata and large numbers of Ceibo trees.

4 (0.08)	% vegetation cover 1-5m (+), Madero (+), Gradient (-), Polopolo (-).	Relatively flat areas with dense low strata where Madero is present and Polopolo absent.

A few species form outliers on one or more axes (Table 4). Black Hawk-Eagle had a very high positive score on Axis 1 (an association with large trees at higher altitudes), while Crested Caracara had a high negative score. Bicolored Hawk had an extreme positive score on Axis 2 (an association with large trees and sparse ground cover) and an extreme negative score on Axis 3 (an association with lower elevation forest with dense lower strata). Several species, namely Black Vulture, Turkey Vulture, Harris´s Hawk, Gray-backed Hawk, Short-tailed Hawk and Laughing Falcon have unremarkable scores on most or all axes indicating that they tend to occupy average habitats. In contrast, Bicolored Hawk appears to have extreme/unusual habitat positions on several axes.

Table 4. Centroid positions for each raptor species on each of the four main CCA axes. Values < 0.10 are not shown.

Species	Axis 1	Axis 2	Axis 3	Axis 4
Turkey Vulture	-0.15			
Black Vulture	-0.27	-0.27		+0.25
King Vulture	+0.54	-0.33	-0.21	+0.40
Bicolored Hawk	+0.49	+1.07	-1.10	+0.88
Crane Hawk	-0.12	+1.33		-0.45
Great Black-Hawk	+0.49		+0.15	
Harris´s Hawk	-0.42			-0.22
Gray-backed Hawk	+0.34		+0.28	
Short-tailed Hawk	+0.35	-0.43	+0.45	-0.40
Zone-tailed Hawk	-0.44	-0.65	-0.85	-0.55
Black Hawk-Eagle	+1.29		+0.29	-0.11
Laughing Falcon			-0.21	-0.30
Crested Caracara	-1.07	+0.35	+0.97	+0.32
Bat Falcon	-0.42	-0.70	-0.36	+0.26

Figure 8. Ordination of habitat variables on the first two canonical axes of CCA. Algarrobo, Faique, Madero, Ceibo, Guasimo, and Polopolo are the numbers of each tree species recorded within the km^2 (see Study area for details of these trees' ecological significance).

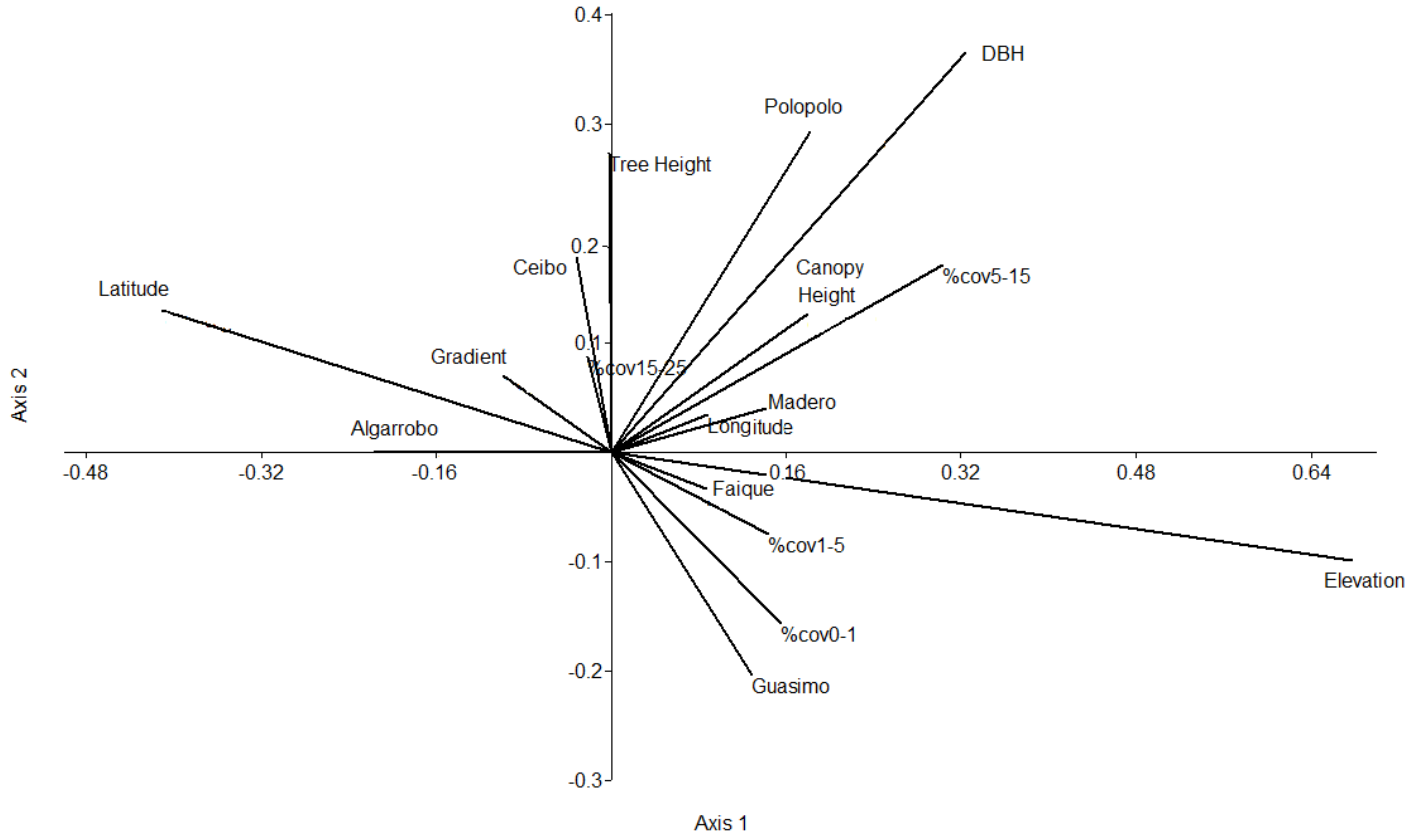
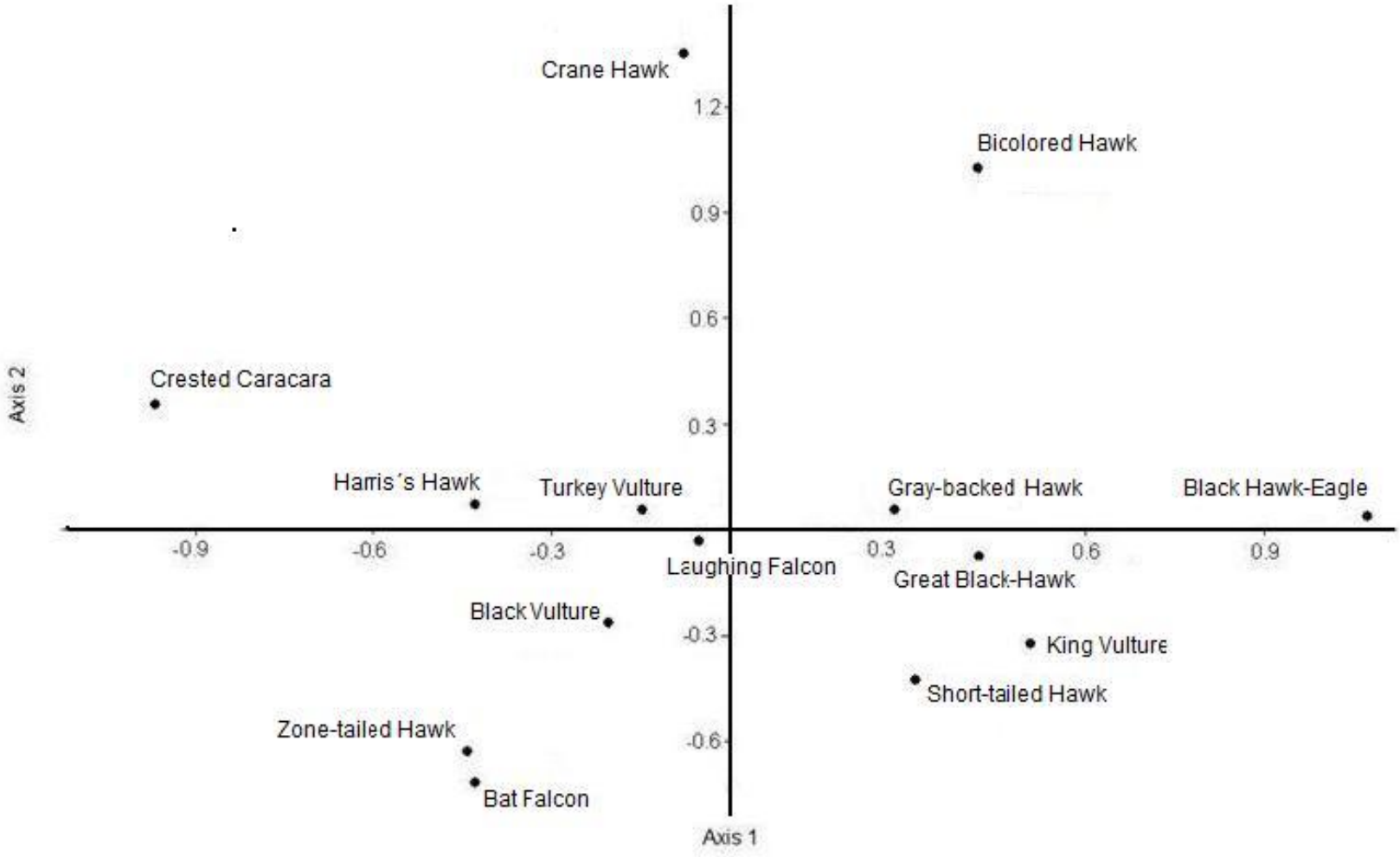


Figure 9. Raptor species ordination in the two first axes of CCA.



3.5.3 *Niche characteristics*

Density estimates (derived using distance sampling and averaged across all samples within the study area), niche width, niche position and bottlenecks are presented for each species in Table 5. As expected, there was a significant negative correlation between species density and habitat niche position (r_s = -0.64; P = 0.02) – common species had centroids usually close to the origin on the four CCA axes.

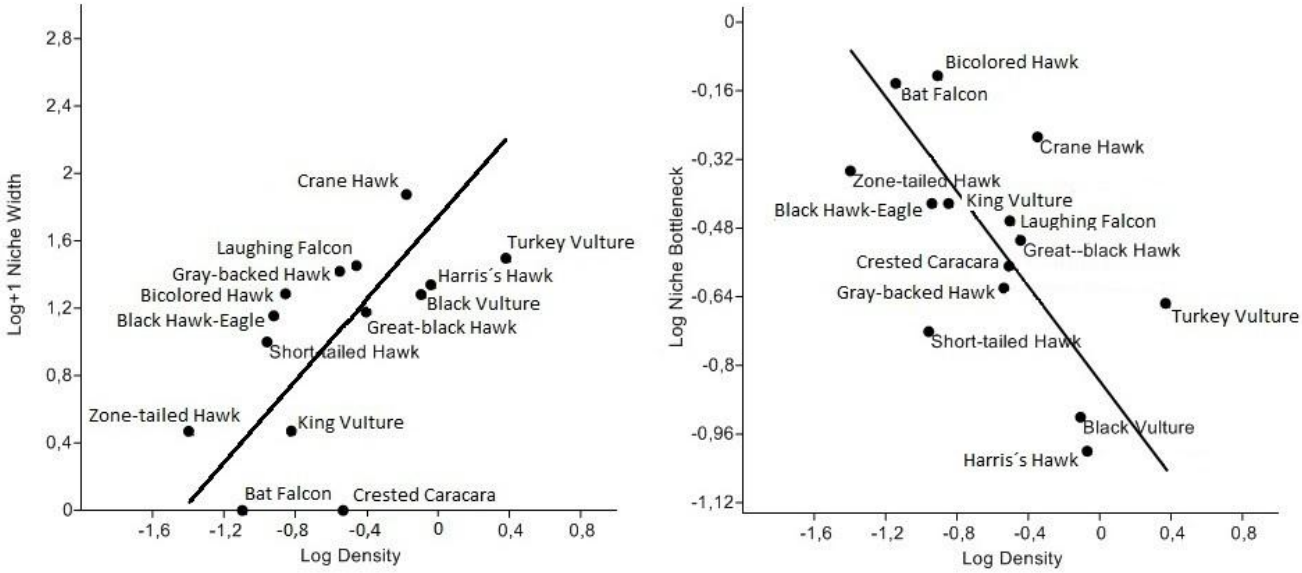
Abundance (density) was positively correlated with niche width (r_s = +0.72; P < 0.01), although there was considerable variation in the abundance-niche width relationship for individual species (Figure 10). Black Vulture had a density estimate only one-third that of Turkey Vulture and yet they had similar niche widths. Of the rare species, Bat Falcon, Zone-tailed Hawk, King Vulture and Crested Caracara had unusually narrow niches and Bicolored Hawk and Crane Hawk relatively wide habitat niches.

Table 5. Density estimates (95% confidence intervals), detection function (DF), niche position, width and bottleneck for raptors in the Tumbes, Peru. Niche bottleneck was calculated as deviation of the minimum niche width on any single axis from the mean niche width (on all four axes) divided by this mean. Thus large values indicate a narrow minimum niche width. Also shown is the axis on which niche width was narrowest. Detection functions and expansion series (DF): Half-normal (HN), Uniform (U), Hazard rate (H), Cosine (C), Polynomial (P), Hermite (He).

Species	Density (Inds. km^{-2})	DF	Niche position	Niche width	Niche bottleneck	
Turkey Vulture	2.4 (1.6-3.6)	UC	0.61	3.14	0.22	AX1
Black Vulture	0.78 (0.49 - 1.3)	HNHe	1.42	1.95	0.12	AX1
King Vulture	0.14 (0.07 - 0.27)	UC	2.24	0.63	0.38	AX1
Bicolored Hawk	0.13 (0.06 - 0.30)	UC	7.27	1.93	0.75	AX1
Crane Hawk	0.49 (0.23 -1.04)	HNC	2.99	7.50	0.54	AX1
Great Black Hawk	0.36 (0.20 - 0.67)	HNHe	1.56	1.60	0.31	AX2
Harris´s Hawk	0.85 (0.57 - 1.3)	UC	0.76	2.10	0.10	AX1
Gray-backed Hawk	0.29 (0.17 - 0.50)	UC	1.89	2.63	0.24	AX1
Short-tailed Hawk	0.11 (0.06 - 0.21)	UC	2.88	1.00	0.19	AX3
Zone-tailed Hawk	0.04 (0.02-0.09)	HNC	3.45	0.29	0.45	AX2
Black Hawk-Eagle	0.12 (0.07 - 0.20)	UC	2.70	1.43	0.38	AX2
Laughing Falcon	0.33 (0.23 - 0.48)	UC	1.29	2.82	0.34	AX1
Crested Caracara	0.31 (0.14 - 0.70)	HP	3.46	0.10	0.27	AX2
Bat Falcon	0.08 (0.03 - 0.17)	UC	2.21	0.10	0.72	AX2

The most important bottlenecks in niche width (those axes where individual species had their narrowest niche) were on Axes 1 and 2. There was a significant positive relationship between degree of bottleneck and overall niche position (r_s = +0.59; P = 0.03) and a negative relationship with abundance (r_s = -0.56; P = 0.04). Again, there was variation across species in the abundance-bottleneck relationship (Figure 10) with the small rare species Crane Hawk, Bat Falcon and Bicolored Hawk having particularly narrow bottlenecks and with Harris´s Hawk, Black Vulture, Short-tailed Hawk, Turkey Vulture, Gray-backed Hawk and Crested Caracara showing little constriction on any CCA axis.

Figure 10. Scatterplot of the relationships between log transformed species densities and log +1 species´ habitat niche width and log transformed species´ bottlenecks. Densities were estimated using distance sampling and are averaged across all 70 one-km^2 squares within the study site.



3.6 Discussion

3.6.1 *Community assemblage*

I was able to separate species in terms of their niche positions and specifically in terms of their associations with environmental variables within the study area. Species preferring habitats with large trees (e.g. Bicolored Hawk) separated from birds that preferred dry forests (e.g. Crested Caracara), and species preferring borders (e.g. Laughing Falcon). Some inferences regarding habitat preferences can be made between community members that share similar morphometric characters: Bicolored Hawks and Crane Hawks, both species with long tails, long tarsi and small body mass (but with different diets – see Thorstrom and Quixhán 2000, Sutter et al. 2001) were associated with very high scores on axis 2 (forest with large trees but sparse ground cover). Black Hawk-Eagle, another species with long tail and a forest specialist (Thiollay 2007) was associated with increasing elevation and was relatively common in high canopy semi deciduous forests, while the morphologically similar Harris´s Hawks were associated with dryer habitats in the lowlands where Algarrobo trees dominated. Gray-backed Hawks and Laughing Falcons similar in body mass, body length and diet (Vargas 1995, Valdez 1996) were relatively abundant in borders but segregated geographically and by elevation, percentage of vegetation cover from 5 to 15 meters, and canopy height.

3.6.2 *Niche relationships*

There was a wide range of variation in habitat niche width among species, and most species appear to be generalists in the use of space. I acknowledge that my inclusion of aerial individuals was not ideal for two reasons. First it may inflate density estimates for the species, although I do not discuss absolute density in this chapter, rather species-specific densities relative to each other, and 'corrected' for differences in detectability with the use of distance sampling (e.g. Buckland et al. 2001). Second, my inclusion of aerial birds means that individuals I recorded over a particular square did not necessarily belong to it since they may be flying over, rather than using the area for hunting. Several studies (Seagle and McCracken 1986, Gregory and Gaston 2000, Marsden and Whiffin 2003) found no relationship between bird abundance and niche width (none of the above focused on raptors). In this study I found a significant positive relationship between habitat niche width and species abundance. Analysis of data from Table 2 in Thiollay´s (1993) study of raptors in India, also reveals a positive significant relationship between habitat niche width and species abundance (r_S = 0.76; P = 0.002) indicating that, in these two raptor communities, species that are able to function in a wider range of habitats are likely to be more abundant overall (Table 5).

Spatial niche overlap (Table 2) indicates how two species shared geographical space with high values indicating more affinities in the use of spatial resources (Pianka 1974). In this study species that were usually detected at borders and degraded areas showed greater niche overlap between them while it was lower between forest interior species. Mantel tests revealed no correlation in spatial

niche overlap between species and body size differences, but there was a near-significant relationship between spatial niche overlap and dietary overlap.

3.6.3 *Conservation implications*

There were significant differences in raptor species diversity and abundance within the three different land use regimes in the study area. Raptors were more diverse and abundant in the buffer areas followed by the reserve and the park, despite the last being under the highest level of protection (SPDA 2004). In extreme northwest Peru protection of forested areas outside the TNR and the CANP can help preserve habitats that are fundamental to maintain this highly diverse raptor community and the species they support. If properly managed, the recently created Tutumo-Matapalo Conservation Area, in the buffer area north of the CANP can help to achieve this.

Kruger and Radford (2008) identified body weight, clutch size and habitat niche width as the three most important variables that predict extinction risk among Accipitridae. Therefore, in this study, species with higher values on habitat niche width (Crane Hawk, Turkey Vulture, and Laughing Falcon) might be of least conservation concern within the community. Great Black Hawks and Black Hawk-Eagles had the highest body mass among Accipitridae, while Gray-backed Hawks had the lowest reproductive rate (0.8 fledged young per nest; Vargas 1995). Black Hawk-Eagles had a lower habitat niche width value and a higher niche position than Great Black Hawks and within the community, is probably the most susceptible to habitat loss, particularly of semi-deciduous forest that in extreme northwest Peru only occur above 600 m in the CANP and

that have been severely destroyed in adjacent Ecuador (Dodson and Gentry 1991; Best and Kessler 1995). Deciduous forests inside the CANP are probably the largest and more continuous tracts of this habitat still remaining in the whole Tumbesian zone and might be crucial for the species persistance in this centre of endemism.

Niche bottlenecks for each species show the greatest constriction of a species' niche width on any of the axes (Table 4). There was a very strong positive relationship between bottleneck width and abundance, with the small rare species Crane Hawk, Bat Falcon and Bicolored Hawk having particularly narrow bottlenecks. This has important implications for conservation management. If I can identify the axis on which a species has its narrowest niche width, then I can use this information to guide habitat management for that species (e.g. Botham et al. 2011). Specifically, I can increase the proportion of habitat within the study area that falls within the range of values (e.g. a range of canopy closure values or the numbers of a preferred tree species) that the species uses. Habitat management that brings extra amounts of land cover within the species' (realised) niche may be more important on the bottleneck axis than on other habitat axes because the species has a narrower range of tolerance on that niche axis. Using the example of Bicolored Hawk above, managing habitat so more areas fall within its niche position on Axis 1 may be most beneficial to it – and this corresponds to increases in higher altitude forest that has large trees and fuller mid-level vegetation cover (see Table 3).

Almost all species in this study were wide ranging occurring over much of the neotropics. In Peru, these species are widespread east of the Andes but are also present in Tumbes. The only range restricted species, the endangered

Gray-backed Hawk (BirdLife International 2011) was the fifth most often recorded species, but had only the eighth highest density estimate (Table 5). This species had an ‘average’ niche position, and had the fourth widest habitat niche with little niche constriction. In Ecuador the species has been recorded in primary and secondary forests, forest borders, and adjacent agricultural and pasture areas along its range (Vargas 1995, Freile et al. 2004) thus supporting the idea that it has a wide habitat niche. Despite this, the species population has, apparently, been in continual decline in Ecuador due to forest destruction for agriculture and cattle ranching (Vargas 1995, BirdLife International 2011). Although it is now evident that the species can use degraded areas, it is not known whether it can breed there, so future research is needed to clarify this.

Chapter 4: Habitat associations within a raptor community in a protected area in northwest Peru

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4.1 Abstract

Little is known about habitat characteristics that influence the distribution of raptors in the neotropics. I used logistic regressions (GLMs) to obtain habitat distribution models for eleven raptor species occurring in the Cerros de Amotape National Park, the Tumbes National Reserve and its buffer areas in extreme northwest Peru. Between May 2008 and December 2009, raptors were surveyed along transects, and associated habitat data collected in 70 randomly allocated 1 square kilometre plots. Twenty eight habitat models were obtained for all species and twelve habitat variables were included. Spatial autocorrelation in the distribution of species was measured through Moran´s *I* and later habitat models were ranked using Akaike´s Information Criterion for small sample size (AICc). Best models obtained for six species included measured percentage of vegetation cover at different strata, while elevation and latitude were included in five. Additionally, sixteen models included variables that measured percentage of vegetation cover and all but two species included an autocovariate. These findings suggest that vertical structure of forested areas is of particular importance for raptors in the study site. For the endangered Gray-backed Hawk, a species associated to semi-deciduous forests east of the study site, I recommend that forest areas north and east of the Cerros de Amotape National Park and close to Ecuador should be protected while cattle grazing in these areas should avoid further destruction of remaining forest patches.

4.2 Introduction

The identification of factors that determine species presence in the landscape is key for the conservation and maintenance of biological diversity (Cleary et al. 2005). In recent years, modeling of species distribution has become an important tool in conservation biology (Guisan and Thuiller 2005; Wu et al. 2006), with General Linear Models (GLM) becoming very popular for predicting species richness and distribution (Lehmann et al. 2002; Syartinilia 2008).

GLM are widely used in applied ecology and conservation ecology to model species distribution with presence and absence data (Guisan and Zimmermann 2000; Guisan and Thuillller 2005; Austin 2007) and recently have been used to model breeding habitat, habitat use and areas of conservation importance for raptor species in temperate environments (Wu et al. 2006; Lopez-Lopez et al. 2007).

Diurnal raptors cover a broad spectrum of ecological requirements and are considered good indicators of changes in ecosystems (Thiollay 2006c) and while habitat destruction is regarded as the most important threat for forest raptors (Thiollay 1985), habitat loss, fragmentation and degradation also affects the survival of tropical species (Thiollay 1993). Understanding how species are distributed in the landscape and which factors may affect such distributions is important for the monitoring and conservation of biodiversity and this knowledge can also be applied to the protection of species (Wu et al 2006).

Habitat modeling of raptors inhabiting temperate ecosystems has contributed to assessing the role of different habitat attributes that influence the occurrence and distribution of single raptor species (Martinez et al. 2003; Donazar et al.

1993), in the design of conservation plans for endangered and non-endangered species (Muñoz et al. 2005; Lopez-Lopez 2007) and to identify habitat variables that better contribute in maintaining the assemblage of the raptor community as a whole (Bustamante and Seoane 2004). However, it seems that no attempts have been made to use similar methods in the construction of habitat models for neotropical raptor species.

Located in extreme northwest Peru, the North West Biosphere Reserve (NWBR) holds a particularly rich assemblage of raptor species (Piana et al. 2010), including the Gray-backed Hawk. Despite its status as a conservation area, forests inside the reserve are subject to several human induced activities such as cattle grazing and logging; particularly in the Tumbes National Reserve and buffer areas, where vast extensions of forest have been removed for the establishment of cattle pastures. It is still uncertain how forest destruction and fragmentation affects raptors distribution in this biome. Modeling raptor species distributions through its relation to habitat variables could help to understand how habitat modifications affect raptors occurrence in this part of the neotropics.

The aims of this chapter are: 1. To identify the most important floristic and geographical variables that influence species presence and that also shape the assemblage of the community in the NWBR, while accounting for spatial autocorrelation. 2. To develop habitat distribution models through the use of logistic regression for a guild of eleven raptor species that inhabit the dry, deciduous and semi-deciduous forests of extreme northwest Peru. 3. To use these models to define management interventions for the species and areas in northwest Peru; particularly those of conservation concern.

4.3 Methods

Data on raptors and associated habitat measures were collected during two field seasons April-December 2008 (31 one-km^2 square plots) and April-December 2009 (39 one-km^2 square plots). All seventy (70) one-km^2 square plots were evaluated in the morning (see Field Methods). Bird-habitat association models were obtained for species of raptors that were recorded in more than 10 km squares. These species were: Turkey Vulture, Black Vulture, King Vulture, Crane Hawk, Great Black Hawk, Harris´s Hawk, Gray-backed Hawk, Short-tailed Hawk, Black Hawk-Eagle, Laughing Falcon, and Crested Caracara. Models were built using a binomial General Linear Model (GLM) (binary logistic regression) between habitat variables and the presence/absence of individuals using SAM 3.1 software (Rangel et al. 2006). GLMs (McCullagh and Nelder 1989) are mathematical extensions of linear models that assume a relationship between the mean of the response variable (raptor species presence) and the linear combination of the explanatory variables (habitat variables) (Guisan et al. 2002). GLMs are suited for analyzing ecological relationships between the mean of a response variable and the linear combination of one or more explanatory variables through regression analyses (Guisan et al. 2002).

4.3.1 Statistical analyses

To reduce any effects of multicollinearity (Zuur et al. 2010), pairs of habitat variables were tested for correlation using Spearman´s rank correlation test in PAST software (Hammer et al. 2001). Pairs of variables with absolute r_s values

higher than 0.75 were considered highly correlated so one variable (the one with less biological sense in the model) was removed from analysis (Lor and Malecki 2006).

In GLMs, the lack of spatial independence in data should be addressed to avoid issues of spatial pseudoreplication (Liebhold and Gurevitch 2002; Dormann 2007). This can be achieved by adding a spatial autocorrelation term to the linear predictor, by sampling at a given spatial distance to avoid autocorrelation or by sampling at the same intensity in areas of known and unknown occurrence of target species (Guisan and Thuillller 2005; Dormann 2007). Spatial autocorrelation, the tendency of neighbouring samples units to be more similar than those expected for randomly associated observations (Lichstein et al. 2002), affects the assumption of independence of samples and of identically distributed errors (Fielding and Bell 1997; Legendre 1993; Dormann et al. 2007), inflating type I errors. I calculated spatial autocorrelation in the distribution of raptor species across the study area through Moran´s *I* (Moran 1950) using Spatial Analysis in Macroecology (SAM) 3.1 software (Rangel et al. 2006). Distances between pairs of squares were grouped into five classes and set to a maximum of 25 kilometres, each class having equal number of pairs. Significance was tested using 200 permutations and a Moran´s *I* correlogram (Legendre 1993) was produced for each species (Figure 11).

Habitat variables selected for analysis were: Latitude, longitude, elevation, gradient, tree height, percentage of vegetation cover between 0 to 1 m, percentage of vegetation cover between 1 to 5 m, percentage of vegetation cover between 5 to 15 m, and presence of Polopolo, Ceibo, Algarrobo and Guasimo trees. Best habitat models were selected using Akaike´s Information

Criterion (AIC) values corrected for small samples (AICc) (Akaike 1973; Burnham and Anderson 2002); only those models with a difference in AICc values of less than two (compared to the model with the lowest AICc value, namely zero) were considered as the best ones and included in the results (Burnham and Anderson 2002). Additionally Akaike weights (Wi); a measure of the strength of each model, sensitivity (the proportion of correctly classified presences) and specificity (the proportion of correctly classified absences) were calculated for each model (Burnham and Anderson 2002).

4.4 Results

4.4.1 Habitat models

All habitat models selected were significant with *P* values ranging from 0.0047 (Gray-backed Hawk) to 0.0001 (Crane Hawk, Black Hawk-Eagle, Crested Caracara). The number of selected models per species, using differences on AICc values (ΔAICc = 2) varied from four (Turkey Vulture, Harris´s Hawk, Laughing Falcon) to one (Great Black Hawk, Short-tailed Hawk and Crested Caracara). In all, 28 models were selected considering all raptor species. Sensitivity of models ranged from 0.875 (Black Hawk-Eagle) to 0.567 (Laughing Falcon) and specificity ranged from 0.917 (Crested Caracara) to 0.50 (Turkey Vulture).

Habitat variables that were related to floristic characteristics (percentage of vegetation cover at different heights, tree height, and tree species) appeared in more models than geographic variables (elevation, inclination, latitude, and longitude). Among floristic variables, percentage of vegetation cover between 5

to 15 m and tree height were significant in six and three models respectively while percentage of vegetation cover from 1 to 5 m was significative in one. Among tree species, Ceibo was significant in three models, Polopolo in two and Guasimo in one. The most important geographical variables in determining raptor species presence and absence were elevation (significant in thirteen models), latitude (significative in five), and longitude (significant in four) (Table 6).

The three vulture species were positively associated with values of ground (0 to 1 m) and mid level (1 to 5 m) vegetation cover, with Turkey Vulture particularly associated with decreasing values of vegetation cover from 5 to 15 m. Of these species, Black Vulture and King Vulture were negatively associated with values of tree height. Best models for carrion feeder always included parameters associated with vegetation cover, except for the Crested Caracara which only included elevation and latitude; both negatively associated with species presence.

Among Accipitridae, elevation appeared in all models obtained for Crane Hawk, Harris´s Hawk and Black Hawk-Eagle. The Gray-backed Hawk was positively associated to longitude and negatively associated to the presence of Algarrobo trees. Great Black Hawk and Short-tailed Hawk were positively associated to Guasimo and the Laughing Falcon negatively to Ceibo trees.

4.4.2 Spatial autocorrelation

Spatial autocorrelation on the distribution of the eleven raptor species that were modeled was low. (Figure 11). Moran´s *I* values ranged from a maximum of

0.062 (Black Vulture) to a minimum of -0.086 (Black Hawk-Eagle). Additionally, *P* values in all correlograms were not significant at any given distance for any species yet it was nearly significant for Black and Turkey Vulture (*P* = 0.056 and *P* = 0.083 respectively) at distances close to 10 km and for Black Hawk-Eagle (*P* = 0.072) at distances close to 13 km. Lower AICc values were obtained with the inclusion of a spatial autocorrelation variable in the logistic regression models of all but two species (Great Black Hawk and Black Hawk-Eagle). Additionally, there was no significative correlation between species body mass and the distance were Moran´s *I* was higher (r_s = -0.42; *P* = 0.2).

Table 6: Habitat models and associated statistics for eleven species of raptors presence/absence in northwest Peru. The + or – indicate the species relationship with the response variable. AICc values are AIC values corrected for small samples; ΔAICc shows the difference between values of AICc best fitting models and that of lower AICc value. Akaike weights (Wi), Sensitivity (Sens.) and Specificity (Spec.) values are shown.

Species	Model No.	Variable	AICc	ΔAICc	Wi	Sens.	Spec.	*P*
Turkey Vulture N = 44	1	-AC^{ns}, +%cov 1_5^{ns}, -%cov 5_15**	84.27	0	0.27	0.841	0.500	***
	2	-AC^{ns}, -%cov 5_15**	84.49	0.22	0.25	0.864	0.538	***
	3	-AC^{ns}, -Inclin^{ns}, +%cov 1_5 ^{ns}, -%cov 5_15**	84.59	0.32	0.24	0.818	0.577	***
	4	-AC^{ns}, -Inclin^{ns}, -%cov 5_15**	84.62	0.35	0.23	0.841	0.577	***
Black Vulture N = 34	1	-AC^{ns}, -Elev*, -TreeH*, +%cov 0_1^{ns}	93.25	0	0.43	0.706	0.639	**
	2	-AC^{ns}, -Elev*, -TreeH*	93.60	0.35	0.36	0.676	0.722	**

	3	-AC^{ns}, -Elev^{ns}, -TreeH**, +%cov 0_1^{ns}, +Algarrobo^{ns}	94.78	1.53	0.20	0.676	0.694	**
King Vulture N = 14	1	-AC*, -Lat*, -TreeH^{ns}, +%cov 1_5*, -Ceibo^{ns}	74.01	0	0.61	0.692	0.807	**
	2	-AC*, +Elev*, -TreeH^{ns}, +%cov 1_5^{ns} ,-Ceibo^{ns}	74.91	0.90	0.38	0.692	0.825	**
Crane Hawk N = 10	1	-AC**, -Elev*, +%cov 5_15*, +Polopolo*	57.71	0	0.59	0.8	0.9	***
	2	-AC*, -Elev*, -%cov 1_5^{ns}, +%cov 5_15*, +Polopolo*	58.46	0.75	0.40	0.8	0.9	***
Great Black Hawk N = 17	1	+Lat**, +Guasimo*	72.68	0	1	0.647	0.679	**

Harris's Hawk N = 32	1	-AC^{ns}, -Elev***, -Lat**, -Long*	89.57	0	0.41	0.719	0.632	***
	2	-AC^{ns}, -Elev^{ns}, -TreeH^{ns}, -Lat^{ns}, -%cov 5_15 ^{ns}	90.97	1.40	0.20	0.781	0.711	***
	3	-AC^{ns}, -Elev***, -TreeH^{ns}, -Lat*, -Long ^{ns}	91.03	1.46	0.19	0.719	0.605	***
	4	-AC^{ns}, -Elev**, -TreeH^{ns}, -Lat^{ns}	91.05	1.48	0.19	0.719	0.605	***
Gray-backed Hawk N = 17	1	-AC^{ns}, +Long**, -Polopolo^{ns}, -Algarrobo^{ns}	76.45	0	0.47	0.706	0.642	**
	2	-AC^{ns}, +Long**, -Guasimo^{ns}, -Algarrobo^{ns}	77.59	1.14	0.27	0.647	0.66	**
	3	-AC^{ns}, +Elev^{ns}, +Long**, -Algarrobo^{ns}	77.67	1.22	0.25	0.765	0.642	**

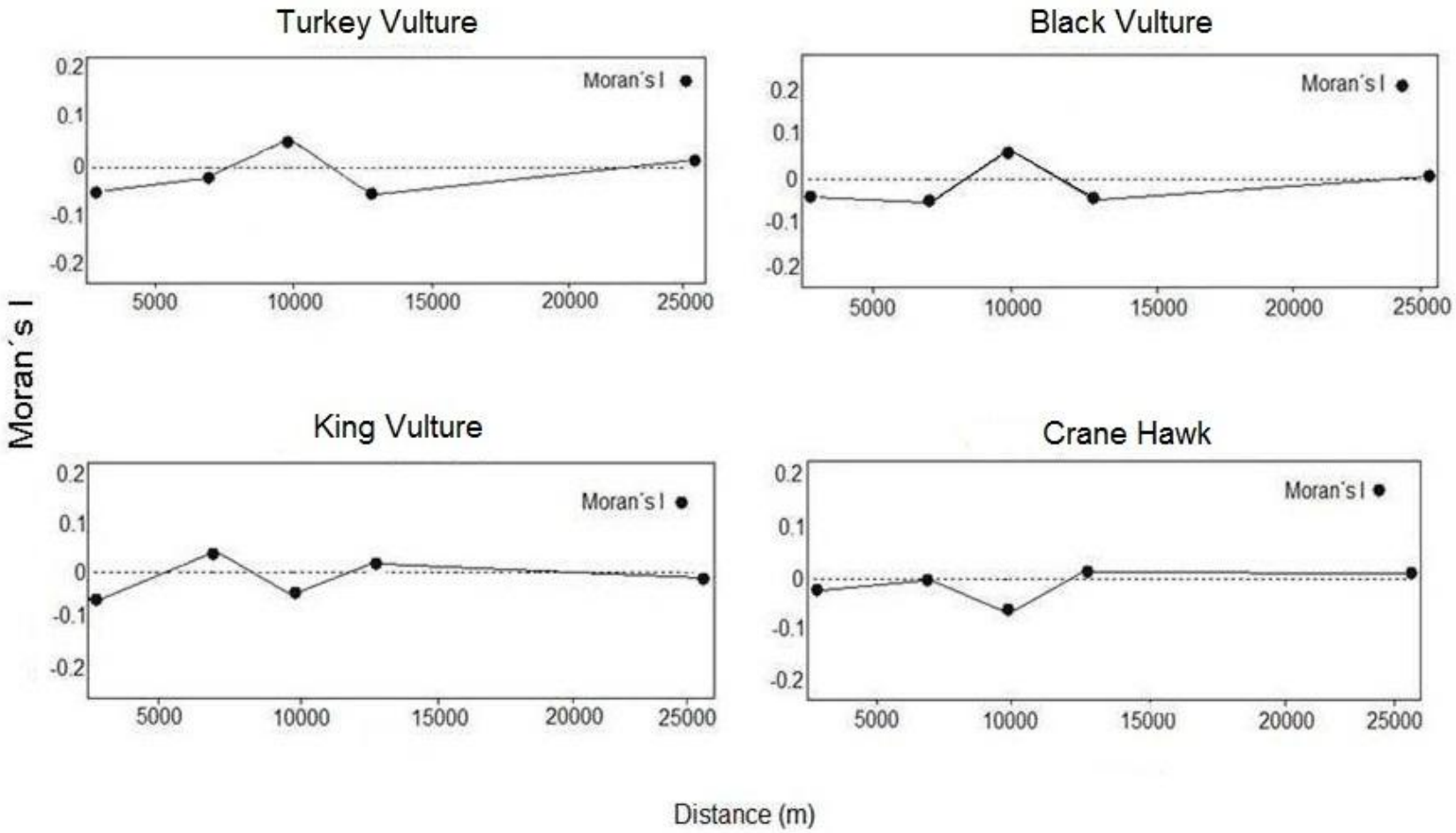
Short-tailed Hawk N = 11	1	-AC*, -Lat^{ns}, +Guasimo**	63.07	0	1	0.636	0.831	**
Black Hawk-Eagle N = 17	1	+Elev***, +%cov 0_1^{ns}	51.65	0	0.39	0.875	0.833	***
	2	+Elev***, -TreeH^{ns}, +Guasimo^{ns}	51.88	0.23	0.34	0.875	0.87	***
	3	+Elev***, +%cov 0_1^{ns}, +Guasimo^{ns}	52.35	0.70	0.26	0.875	0.852	***
Laughing Falcon N = 30	1	-AC^{ns}, -%cov 5_15^{ns}, -Ceibo^{ns}, +Polopolo^{ns}	92.03	0	0.31	0.667	0.80	**
	2	-AC*, -%cov 5_15^{ns}, -Ceibo*	92.16	0.13	0.29	0.567	0.70	**
	3	-AC*, -Ceibo**, -Guasimo^{ns}	92.23	0.20	0.27	0.667	0.725	**
	4	-AC**, -%cov 0_1^{ns}, -%cov 5_15^{ns}, -Ceibo**, +Polopolo^{ns}	93.81	1.78	0.12	0.60	0.70	**

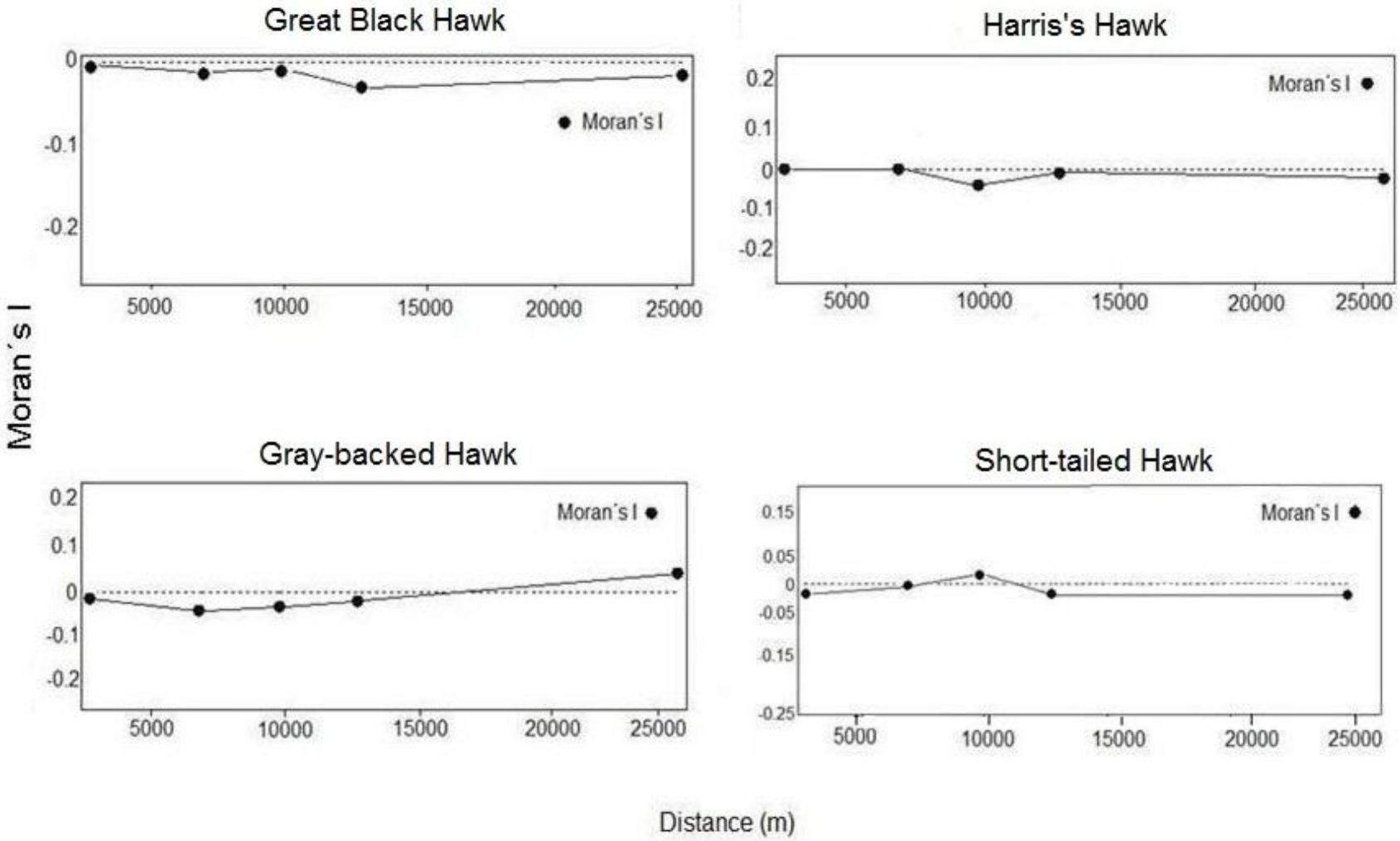
Crested Caracara	1	-AC*, -Elev*, -Lat**	42.46	0	1	0.7	0.917	***
N = 10								

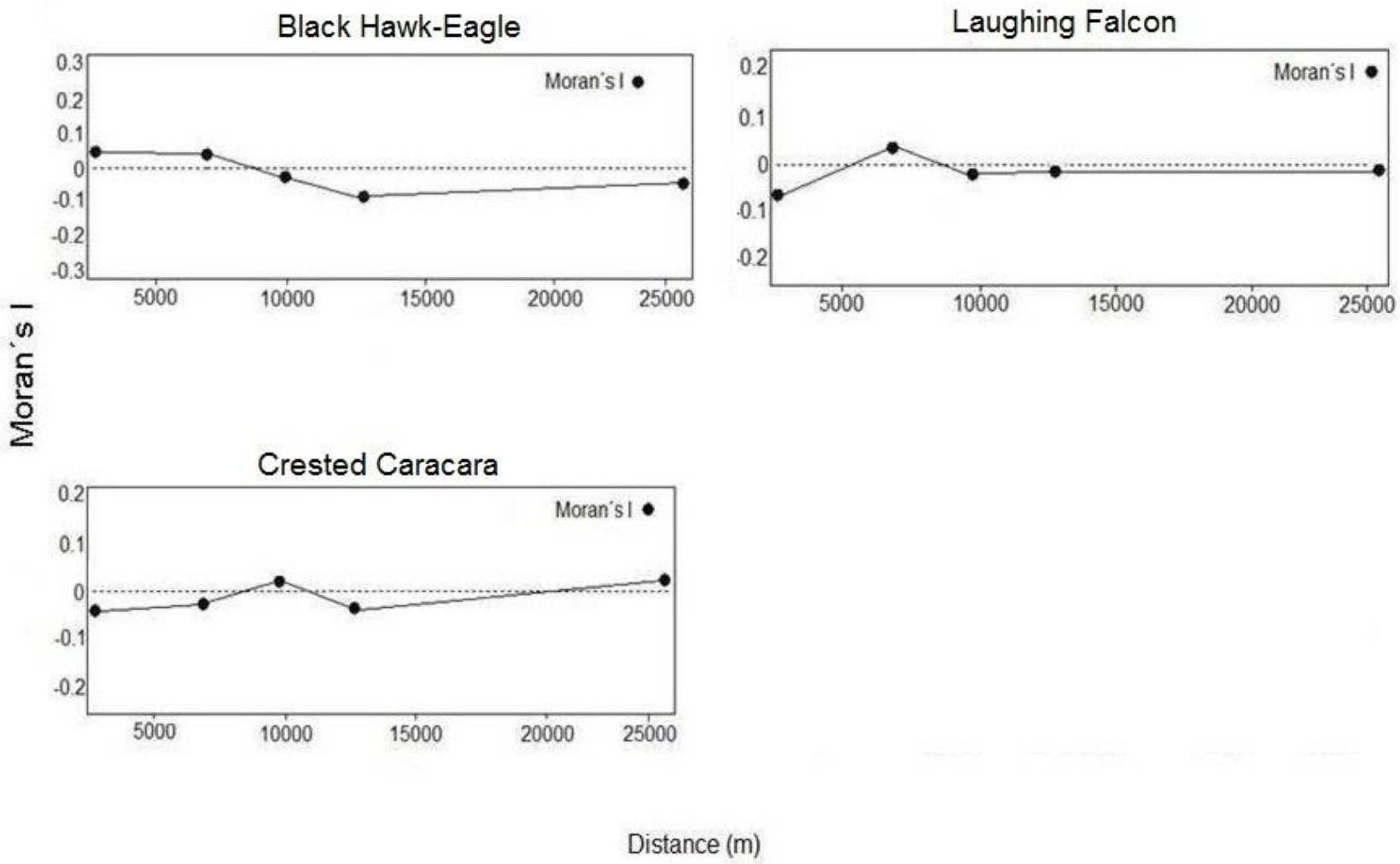
AC= auto covariate term; %cov 0_1= percentage of vegetation cover from 0 to 1 m; %cov 1_5 = percentage of vegetation cover from 1 to 5 m; %cov 5_15 = percentage of vegetation cover from 5 to 15 m; TreeH = Tree height; Lat = Latitude; Long = Longitude; Elev = Elevation; Inclin = Gradient; Algarrobo, Ceibo, Guasimo and Polopolo are the names of each tree species. See the Study area section for a more detailed description.

NS, not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Figure 11: Moran´s *I* Correlograms for eleven species of raptors from northwest Peru. Axis X show distance in kilometers and Axis Y show values of Moran´s *I.*




Great Black Hawk
Harris's Hawk
Gray-backed Hawk
Short-tailed Hawk
Moran´s I
Moran´s I
Distance (m)
0
-0.1
-0.2
0.2
0.1
0.15
0.05
-0.05
-0.15
-0.25
5000
10000
15000
20000
25000


Black Hawk-Eagle
Moran´s I
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
5000
10000
15000
20000
25000
Laughing Falcon
Moran´s I
0.2
0.1
0
-0.1
-0.2
5000
10000
15000
20000
25000
Crested Caracara
Moran´s I
0.2
0.1
0
-0.1
-0.2
5000
10000
15000
20000
25000
Moran´s I
Distance (m)

4.5 Discussion

4.5.1 Habitat models

Distribution of raptor species in the environment are a consequence of several interacting variables (Janes 1985; Potapov 1997). In this study, the best habitat models pooled across all species, featured eleven variables with gradient being the only one excluded. Among these models, percentage of vegetation cover at different strata appeared in six and latitude and elevation in five. Among all models selected, percentage of vegetation cover at different strata (0 to 1 m, 1 to 5 m and 5 to 15 m) and elevation appeared in those obtained for seven species, and seemed to be the most important habitat variables to influence species presence in extreme northwest Peru. Vegetation cover might enhance or restrict raptor species presence by influencing prey detectability, the availability of perching and nesting sites, and may influence the general features of hunting areas (Bechard 1982; Preston 1990; Williams et al. 2000). In extreme northwest Peru, elevation and latitude are related to the presence of different habitat types with taller and vertically more complex forest occurring at higher elevations (Aguirre et al. 2006). The inclusion of these two habitat variables in species´ best models might also be an indication of the importance of vegetation structure in influencing the presence of raptor species in the study site.

Lowland dry forests were more abundant in the northwestern side of the study site where Algarrobo trees dominated, and structurally more complex and taller deciduous and semi-deciduous forests, with presence of Guasimo, Polopolo and Ceibo trees were typical of the hills located in the south and central portions

of the study site above 100 m (Aguire et al. 2006). Models obtained for King Vulture, Crane Hawk, Great Black Hawk, Gray-backed Hawk, Short-tailed Hawk, Black Hawk-Eagle and Laughing Falcon included these tree species and might be particularly important for their occurrence in the study area and for the maintenance of the raptor community assemblage.

4.5.2 Spatial autocorrelation

Spatial autocorrelation in species distribution is commonly caused by biological processes that can result in aggregation of individuals (Carroll and Johnson 2007; Dormann et al. 2007). Among raptor species, territory occupancy, nest site selection and dispersal of individuals can be significantly affected by inter and intra-specific interactions that segregate individuals (Katzner et al. 2003, Kruger 2002; Hakkarainen et al. 2004) or aggregate them (Wallace and Temple 1987) and thus influencing their spatial distribution. In this study, I did not find significantly high levels of spatial autocorrelation in the presence/absence of any of the raptor species included in the analysis suggesting that in general, there was no clustering in the record of individuals and, despite the size of the study area, it is probable that their distribution was not limited by their dispersion abilities. Correlograms obtained for only three species showed *P* values close to significance at distance between 10 to 13 km: Turkey and Black Vulture were the two most abundant species in the study site (present at 44 and 34 plots respectively) and were the only ones usually detected in small groups while foraging and searching for food. Aditionally, the Black Hawk-Eagle was restricted to scarce semi-deciduous forests above 600 m where single individuals were detected in soaring flights performed with abundant

vocalizations; a behavior probably related to interspecific territorial segregation. Additionally I frequently observed aggressive interactions between several raptor species that harassed each other during flight and that usually ended with one individual leaving the area. Although the data obtained was not intended to measure competition between species, it is possible that inter and intra specific aggressive behavior between members of the raptor community of extreme northwest Peru affects species and individuals in the use of space, limiting their aggregation which is reflected in the lack of significant spatial autocorrelation. This is also supported by the fact that species in the study site did not present a high number of positives at any given plot that was evaluated.

4.5.3 Conservation implications

Habitat use studies on birds are becoming more important as they incorporate habitat information into conservation planning (Jones 2001). Habitat models obtained here have identified twelve habitat parameters that are related to the presence of eleven species of raptors inside and outside two protected areas in the core of the Tumbesian Centre of Endemism of extreme northwest Peru. These models can be used as tools to implement and strengthen conservation initiatives for single raptor species and the raptor community as a whole through the management and conservation of identified key habitat parameters in the study site. Protection of raptors species through the conservation of its habitats can be used as an indirect approach to protect other species, increasing the value of these models. Additionally, habitat models for raptors can also be used to identify biodiversity conservation corridors and networks more efficiently (Sergio et al. 2006). For raptors in extreme northwest Peru, design and

implementation of conservation initiatives should prioritize habitat parameters related to forest structure such as percentage of vegetation cover at different heights.

Habitat models obtained here can be used to improve the conservation value of particular areas inside the TNR, the CANP and their buffer zones through the management of forest patches where human induced activities have altered vegetation composition and forest structure that favour the presence of raptor species. Additionally, these models can also be used to assist in the creation of other protected areas in extreme northwest Peru and in the Tumbesian Centre of Endemism as they point at key habitat features that are relevant for at least one endangered species of raptor that is endemic to this severely threatened ecosystem and whose population is decreasing throughout its entire range (BirdLife International 2010).

Deforestation and burning of forests associated to cattle grazing is regarded as one of the major threats for raptors in Colombia (Thiollay 1991). This activity is widely conducted inside some portions of the NWBR, affecting the structure and composition of the forests at several strata and thus might be influencing the distribution of certain raptor species (Barnard 1987; Petit et al. 1999; BirdLife International 2010). Among the raptor species that were included in this research, the Black Hawk-Eagle and the Gray-backed Hawk were the ones of higher conservation concern. Black Hawk-Eagle is a rare species west of the Andes in Ecuador and north Peru (Ridgely and Greenfield 2001; Schulenberg et al. 2007) and in the study site was almost exclusively detected on semi-deciduous forests and positively associated to vegetation cover between 0 to 1 m. Additionally, models obtained for *S. tyrannus* consistently showed the

species positive association with elevation and the presence of Guasimo trees. The Black Vulture, the second most abundant species in the study site, was negatively associated with tree height and positively with percentage of vegetation cover from 0 to 1 m. Semi-deciduous forests with Guasimo trees associated to dense understory might constitute key habitat features for the Black Hawk-Eagle in extreme northwest Peru, while absence of tall trees associated to dense understory (a typical feature of cattle pastures) might favour the occurrence of Black Vultures. Transforming semi-deciduous forest patches into cattle pastures in the study site may favor the occurrence of Black Vultures while reducing habitat availability for Black Hawk-Eagles. Further conversion of semi-deciduous forests in extreme northwest Peru should be strictly controlled in order to maintain enough habitat for this species.

The Gray-backed Hawk is an endangered and endemic species with a declining population in Ecuador (BirdLife International 2010; Vargas 1995). In the study site, the most important habitat variable for this species was longitude. Additionally the species was negatively related to the presence of Algarrobo trees, indicating that deciduous forests east of the study area and adjacent to Ecuador are most suitable for this hawk. These forest portions are mostly outside any protected area and are being continually converted into cattle pastures and agricultural lands. Although a proposal for the creation of a Regional Protected Area is being implemented north of the CANP, efforts to protect remaining forest in the north and central parts of the TNR and adjacent Ecuador should be conducted to reduce further conversion and degradation of forest patches and to protect forested corridors that help to maintain connectivity between populations at both sides of the border. This might

enhance the conservation of Gray-backed Hawk in extreme northwest Peru and adjacent Ecuador.

Chapter 5: Densities and population sizes for raptors in a protected area in northwest Peru: Use of Distance Sampling and a review of survey methodologies

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5.1 Abstract

Estimates of density and population size for raptor species are fundamental in assessments of population trends and ultimately in informing their conservation management. In most research, abundance of raptors is expressed as indices of relative abundance, although it is known that these can be poor correlates of actual species density. I calculated density and population size estimates for 15 diurnal raptor species using distance sampling line transect counts in four different habitat types in extreme northwest Peru. Species´ densities were stratified by time of detection (morning or afternoon) and by habitat type. Flying birds were included in the analysis, given the intrinsic low abundance of most raptor species in the study area, and the fact that most flying birds were circling a point. The efficacy of including aerial records is discussed. For all but two species, density estimates were higher in the morning than in the afternoon. Absolute density was higher than 1 individual km^{-2} for three species and for seven species it lay between 0.34 and 0.86 individuals km^{-2}. Most species showed marked preferences for particular habitats. Absolute density of the endemic and endangered Gray-backed Hawk (*Leucopternis occidentalis*) was estimated to be 0.51 individual km^{-2} (SE = 0.14). I argue that transect counts for raptor density estimates performed well for larger species in northwest Peru and the method is recommended for population studies across the Falconiformes.

For smaller, less conspicuous species, however, a point count method with the use of playbacks may render better results.

5.2 Introduction

Most tropical raptors are secretive forest dependant species that naturally occur at low densities and thus are difficult to survey. It is also difficult to get large number of records necessary for analysis (Fuller and Mosher 1987; Thiollay 1989b). Despite their importance, data on population sizes and density for many tropical raptor species are scarce and is particularly missing for species living in areas of conservation priority (Thiollay 1994; Bildstein et al. 1998; Myers et al. 2000). In the neotropics, this is highly relevant because 45% of all raptor species are threatened by habitat loss, fragmentation and degradation (Thiollay 1994; Bildstein et al. 1998).

Transects, point counts and territory mapping are among the principal techniques used to counts birds (Bibby et al 1992), and while several methods have been proposed to estimate relative abundance of raptor species, most research has concentrated on counting raptors along transects or roads which might not be randomly positioned as a way to obtain indices of raptor abundance (Fuller and Mosher 1987; Millsap and LeFranc 1988). These methods may well be biased as bird detectability is affected by observer ability, environmental variables and /or bird behavior, and these factors should be taken into account if absolute density is to be estimated (Anderson 2001; Rosenstock et al. 2002).

Distance sampling is a family of methods used for estimating the density of biological populations in which the observer conducts standardized surveys along (usually) randomly positioned lines or at points, and involves measuring the distance from the observer to each object detected (Thomas et al. 2002). An advantage of distance sampling over index counts (encounter rates) is that it provides direct estimates of densities that are not confounded by detectability (Rosenstock et al. 2002). In distance sampling not all objects will be detected by the observer but a fundamental assumption is that all objects that are on the line or point are detected [g(0)=1]. Since detection probability generally decreases with increasing distance, a detection function based on the number of objects detected at different distances is used to estimate the detection probability of an object at a given distance from the line (Buckland et al. 1993). This detection function is then used to estimate the proportion of objects missed during the survey and to convert count data into an estimate of absolute density (Rosenstock et al. 2002; Thomas et al. 2002; Bachler and Liechti 2007).

For the reliable estimation of densities, two other assumptions should be met during distance sampling: i) objects should be detected at their original location before they move in response to the observer and ii) distances from the object to the line (or point) are measured accurately. Additionally, it is critical that the lines or points are randomly positioned regarding the distribution of the objects that will be surveyed (Hanowski et al. 1990; Buckland et al. 1993; Thomas et al. 2002; Thomas et al. 2010). Distance sampling has been used to obtain absolute densities of bird species in temperate and tropical ecosystems through point counts (Marsden 1999; Lee and Marsden 2008) and transect counts (Shankar Raman 2003) but few attempts have been made to calculate the absolute

density of raptor species in temperate or tropical environments using distance sampling (Andersen et al. 1985; Hall et al. 1997; Boano and Toffoli 2002). Compared to point counts, transect counts cover more ground per unit of time and tend to record more birds because these are registered all along the transect. Transect counts are better suited for species that occur at low densities and might be more appropriate for surveying raptors (Bibby et al. 1998; Buckland et al 2008). However, it is more difficult with transects to meet the assumption that all animals are detected at zero metres particularly in habitats with dense and high forest (Bibby et al. 1998).

Given the accelerated rate of forest destruction and fragmentation in tropical regions (Myers et al. 2000), there is an urgent need to develop new research techniques that while not being resource/time consuming, provide reliable information on raptor density and population size. This can then be incorporated into IUCN Red List assessments of the status of raptor species to properly implement conservation efforts when necessary (Thiollay 1989; Thiollay 1994). The aim of this chapter is to evaluate the effectiveness of line transect distance sampling as an approach to calculate absolute densities of fifteen neotropical raptor species in forested areas of extreme northwest Peru. The aims of this chapter were: 1. To obtain density estimates and population size of 15 raptor species that occur in the study area with the use of distance sampling methods along transects 2. To improve density estimates of rarer species by clustering them with more abundant ones. 3. To obtain density and population size of species in different habitats by using habitat types as a covariate in Multicovariate Distance Sampling (MCDS).

5.3 Methods

Nineteen species of raptors were detected but only fifteen were included in estimations of absolute abundance (those species that were registered more than seven times). Species included were Turkey Vulture, Black Vulture, King Vulture, Harris´s Hawk, Gray-backed Hawk, Great Black Hawk, Black Hawk-Eagle, Crane Hawk, Short-tailed Hawk, Zone-tailed Hawk, Bicolored Hawk, Savanna Hawk, Crested Caracara, Bat Falcon and Laughing Falcon.

5.3.1 Encounter rates of species

Encounter rates per species, an indicator of how frequently a species was encountered in the study area were calculated as the sum of the number of individuals detected on a given transect or road divided by the length of that transect or road. To increase sample size, I included individuals detected randomly when traversing roads and trails inside the study area and then calculated the length of traverse with ArcView 6.2 (ESRI 1999). Figures are expressed as number of individuals per 100 km.

5.3.2 Absolute densities of species

Absolute density of raptor species registered during morning and afternoon transect evaluations were analyzed together and then separated by time of detection to produce species-specific detection functions. These analyses were run through Conventional Distance Sampling (CDS) in DISTANCE 6.0 (Thomas et al. 2010) software. Detection curves and absolute densities of raptor species were obtained by running the analysis with uniform, half normal and hazard rate

key functions with cosine, hermite polynomial and simple polynomial series expansion (Buckland et al. 1993; Thomas et al. 2010). Key function selection was done using Akaike´s Information Criterion (AIC) minimisation and chi-square statistic was used to assess the goodness of fit of each function (Buckland et al. 1993). Determination of values of truncation and grouping of records into distance intervals followed visual inspection of detection histograms under different analysis conditions (Buckland et al. 1993).

I used Multiple Covariate Distance Sampling (MCDS) in DISTANCE 6.0 (Thomas et al 2010) to calculate absolute density of raptor species per habitat type (Marques et al. 2001). MCDS allows for the inclusion of covariates other than distance in the detection function. This is done because many variables (i.e. habitat, observer, flock size, etc.) can affect the detection probability and their inclusion as covariates in the detection function model reduces bias or increases precision of density estimates (Marques and Buckland 2003; Marques et al. 2007). The inclusion of covariates is also a useful approach to estimate density for a subset of data with few observations (Marques and Buckland 2003; Thomas et al. 2010). Detection curves and absolute densities were obtained by running the analysis with half normal and hazard rate (the only key functions allowed in MCDS) with cosine and hermite polynomial series expansion. Models with lowest AIC values were selected. Truncation of outliers was set at 300 m because it was considered the maximum distance at which birds could be identified accurately to species level.

To obtain population size estimates per species and per habitat type, I calculated the area in square kilometres of each habitat type with ArcGis 9.0 (ESRI 2004). For this I obtained an Aster satellite image (Digital Elevation

Model) version 2 of the study area with a spatial resolution of 15 m. I then overlaid a shapefile of the study area with this image and fixed elevation ranges according to habitat types to obtain areas of habitat polygons. I used absolute density for each species in each habitat type and multiplied this by the area of each habitat polygon to calculate population sizes of 15 raptor species in each habitat. The total population size for each species in the study area was the sum of the number of individuals in each habitat type. Minimum and maximum population sizes per species were obtained from the sum of upper and lower confidence intervals of density estimates in each habitat (Jacobs and Walker 1999; Lloyd 2008).

5.3.3 Estimating density in rare species

The number of records recommended for reliable density estimates with Distance analysis is around 100 (Buckland et al. 1993; Marsden 1999). Cluster analysis, a statistical technique used to generate categories fitting a set of observations to identify relationships between samples (Rasmussen 1992; McKenna 2003) was used to group different raptor species with similar detectability coefficients as a way to improve density estimates of very rare species or species difficult to detect that had low numbers of detections and poor detection functions. Coefficients were obtained from information provided by five ornithologists (Fernando Angulo, Daniel Lane, Sebastián Oré, Jose Rojas, Renzo Zeppilli) with extensive field experience in the study site. They were asked to rank fifteen species according to four features that were suspected to affect species detectability. These were: size (total length), soaring behaviour (how much of the day the species spends soaring), vocalization (how

common it is to hear the species calling) and visual conspicuousness (how the species' general colouration and behaviour conceals it or not amongst vegetation) (Rosenstock 2002). I used Ward´s method (Ward 1963) of hierarchical cluster analysis, a technique based on analysis of variance to measure the distances between clusters in the PAST software (Hammer et al. 2001), to produce a dendrogram grouping species with similar detectability. Species in a given group were treated as a single 'species' and their densities obtained with CDS. I then obtained multipliers from detection functions of these 'species'. Absolute densities of each species within a group was obtained with a these multipliers in CDS in DISTANCE 6.0 (Thomas et al 2010).

5.4 Results

5.4.1 Encounter rates for species

The four species with the highest encounter rates (Black Vulture, Turkey Vulture, Harris´s Hawk and Gray-backed Hawk) accounted for 857 (68%) of all 1,261 individuals detected (Table 7). Individuals of the four least commonly encountered species (Zone-tailed Hawk, Bicolored Hawk, Crested Caracara and Savanna Hawk) accounted for just 63 (5%). Less encountered species were Bicolored Hawk and Savanna Hawk. There was a near-significant positive correlation between species total body length/body mass and their encounter rates (r_s = +0.47; P = 0.08; r_s = +0.50; P = 0.06 respectively), yet there was no significant correlation between species wing spans or tail lengths and their encounter rates (r_s = +0.32; P = 0.23; r_s = +0.21; P = 0.45 respectively).

Table 7. Encounter rates per species (number of individuals per 100 km) and standard error (SE), and number and percentage of individuals detected perched or flying during transect counts and random encounters.

Species	Encounter Rate (SE)	Perched (%)	Flying (%)
Turkey Vulture	16.0 ± 0.01	19 (6.5)	273 (93.5)
Black Vulture	30.7 ± 0.08	48 (14.4)	285 (85.6)
King Vulture	3.3 ± 0.003	5 (7.3)	64 (92.7)
Bicolored Hawk	0.6 ± 0.02	10 (83.3)	2 (16.7)
Crane Hawk	2.1 ± 0.003	30 (85.7)	5 (14.3)
Savanna Hawk	0.4 ± 0.01	7 (63.6)	4 (36.7)
Great Black Hawk	2.4 ± 0.003	26 (55.3)	21 (44.7)
Harris´s Hawk	6.6 ± 0.007	75 (62.0)	46 (38.0)
Gray-backed Hawk	5.9 ± 0.006	32 (28.1)	82 (71.9)
Short-tailed Hawk	1.4 ± 0.02	4 (14.3)	24 (85.7)
Zone-tailed Hawk	1.0 ± 0.02	0 (0.0)	20 (100.0)
Black Hawk-Eagle	2.9 ± 0.005	6 (13.6)	38 (86.4)
Laughing Falcon	5.3 ± 0.09	82 (96.5)	3 (3.5)
Crested Caracara	1.3 ± 0.02	18 (58.1)	13 (41.9)
Bat Falcon	1.4 ± 0.04	17 (89.5)	2 (10.5)

5.4.2 Perched and flying detections

All individuals of Zone-tailed Hawk were detected in flight. Species like Turkey, Black and King vultures, Black Hawk-Eagle and Short-tailed Hawk had very high percentages (> 85%) of individuals detected flying, while high percentages (> 80%) of individuals of Crane Hawk, Laughing Falcon, Bat Falcon and Bicolored Hawk were detected perched. There was a highly significant positive relationship between percentage of individuals detected flying and species with larger wing spans (r_S = +0.74; P = 0.002). There was also a significant positive relationship between species size and body mass and percentage of individuals that were detected flying (r_S = +0.60; P = 0.02 and r_S = +0.61; P = 0.02 respectively). However there was no correlation between encounter rates and percentages of individuals detected flying (r_S = +0.22; P = 0.42).

5.4.3 Absolute density of raptors

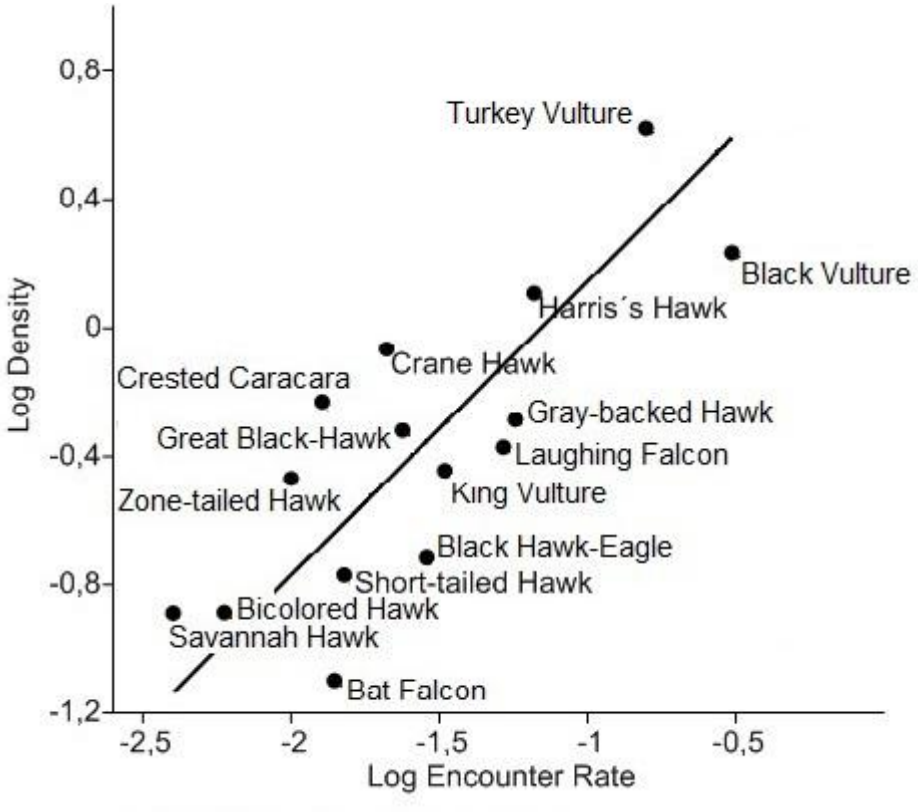
The total number of raptor detected during transect counts was 633 (AM and PM pooled), and number of detections per species varied between 168 (Turkey Vulture) and 5 (Savanna Hawk) (Table 8). Only two species (Black and Turkey vulture) had more than 100 records, while three species, Harris´s Hawk, Gray-backed Hawk and Laughing Falcon had between 40 and 68 records. Seven species had 10-39 records and three species had fewer than 10. Density (individuals km^{-2} ± %CV) of all raptor species combined was 9.7 ± 7.5% (AM and PM transects pooled together). Absolute density of Turkey Vulture was the highest of all species in all pooled transects (4.1 ± 16.5%) and separated (3.9 ± 18.9% in the morning and 4.1 ± 26.6% in the afternoon). In all pooled transects,

percentage of coefficient variation of absolute density for nine species was less than 30% and for two species was 31-34%. Only four species had %CV ranging from 37% to 56% and except for the Zone-tailed Hawk, all of these were not detected in the afternoon.

The Gray-backed Hawk had an absolute density of 0.51 ± 27.8% individuals km^{-2} which was similar to that of the Great-Black Hawk (0.47 ± 28.8%). The density estimate for Black Hawk-Eagle and Short-tailed Hawk were among the lowest (0.19 ± 23.5% and 0.16 ± 25.1% respectively). Number of detections for Bicolored Hawk, Bat Falcon and Savanna Hawk were probably too low to obtain reliable density estimates, and these ranged between 0.18 and 0.21 with %CV above 50%.

There was a significant positive correlation between encounter rates of species and species´ absolute densities (r_S = +0.73; P < 0.01), however there were variations in the relationship of species density and their encounter rates. Crested Caracara had similar encounter rates to Bat Falcon yet its density estimate was four times higher, while density of King Vulture was similar to that of Zone-tailed Hawk yet the vulture´s encounter rate was three times higher (Figure 12).

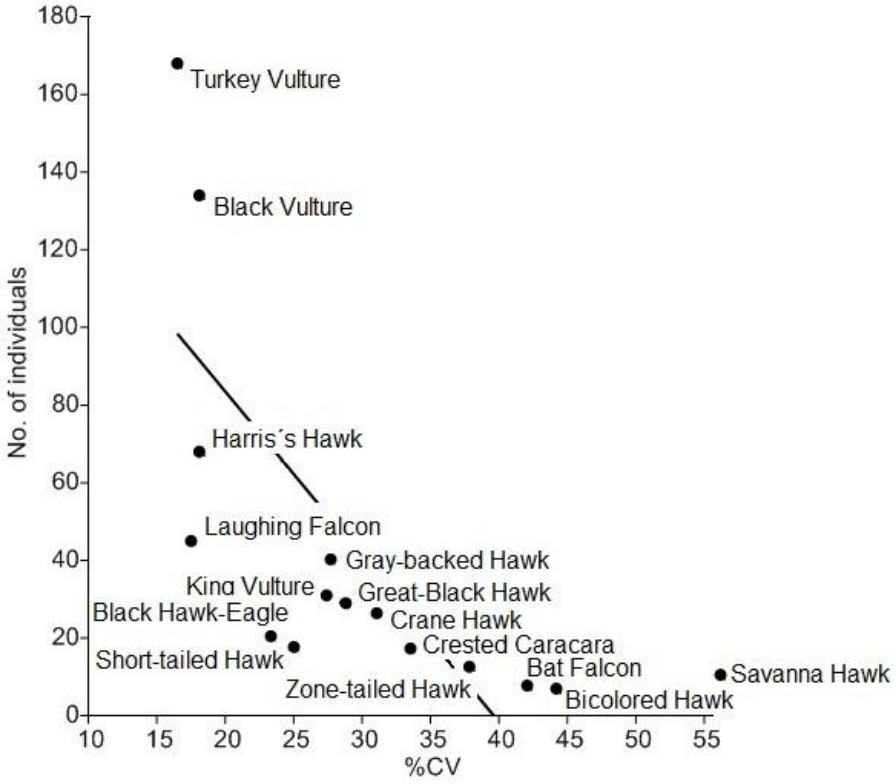
Figure 12: Scatterplot of the relationship between of log transformed density estimates per species and log transformed encounter rates.



5.4.4 Number of records and precision of density estimates

There was a strong negative correlation between number of detections per species and the values of %CV of their density estimates (r_s = -0.89; $P < 0.001$; Figure 13). Turkey and Black vultures (168 and 134 detections respectively) had %CV between 16 and 19%; a very similar %CV was obtained by the density estimate of Harris´s Hawk, although the number of detections for this species was 68.

Figure 13: Scatterplot of the relationship between number of individuals detected per species and percentage of coefficient variation of density estimates.



Several species, namely King Vulture, Crane Hawk, Great Black Hawk, Short-tailed Hawk, Black Hawk-Eagle and Crested Caracara had %CV of their density estimates close to 30% despite the number of individuals detected were around 30 or below. However, in general, it would be necessary to obtain between 40 to 80 records per species to produce density estimates with CV of 20 to 30%.

5.4.5 Effect of time of day on density estimates

Density of all raptors (species combined) was lower in the morning than in the afternoon (8.7 ± 8.9% individuals km^{-2} vs. 12.0 ± 6.6%). This was also observed at species level except for the Great-Black Hawk and Zone-tailed Hawk. There was a significant difference between %CV of densities obtained at different times of day, with higher values for species detected in the afternoon (t = 5.64, n = 11, P < 0.001). I did not detect any individuals of Bicolored Hawk, Bat Falcon and Savanna Hawk in the afternoon and except for the Black and King vultures, more detections were made in the morning than in the afternoon (Table 8).

Table 8. Number of detections (n), absolute density (D) in number of individuals km^{-2}, percentage coefficient variation (CV) and 95% confidence interval (C.I.) of raptor species from transects counts evaluated in the morning (AM) and in the afternoon (PM) and both evaluations pooled together (AM+PM). Detection functions and expansion series (DF): Half-normal (HN), Uniform (U), Hazard rate (H), Cosine (C), Polynomial (P), Hermite (He).

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	AM					PM					AM+PM				
Species	n	D	CV	95% C.I.	DF	n	D	CV	95% C.I.	DF	n	D	CV	95% C.I.	DF
All	412	8.72	8.9	7.3–10.4	HNC	221	12.0	16.6	8.6–16.7	HP	633	9.74	7.5	8.4 – 11.3	UC
Turkey Vulture	107	3.94	18.9	2.7–5.7	HNC	61	4.10	26.6	2.4–6.9	HNC	168	4.10	16.5	3.0–5.7	HNC
Black Vulture	63	1.17	23.2	0.8–1.9	HNH	71	2.92	26.1	1.7–4.9	UC	134	1.72	18.1	1.2–2.5	HNC
King Vulture	15	0.21	32.7	0.1–0.4	UC	16	0.80	36.5	0.4–1.6	UC	31	0.36	27.4	0.2–0.6	HP

Bicolored Hawk	7	0.18	52.3	0.1–0.5	HNC	0	0	0	0		7	0.13	43.9	0.1-0.3	UC
Crane Hawk	15	0.74	38.4	0.4-1.6	HNC	11	1.10	51.9	0.4–2.9	HNC	26	0.86	31.1	0.5–1.6	HNC
Savanna Hawk	5	0.19	55.2	0.1-0.6	HNHe	0	0	0	0		5	0.13	55.4	0.04-0.4	HNC
Great Black Hawk	24	0.54	31.0	0.3-1.0	HNHe	5	0.38	73.8	0.1–1.5	HNHe	29	0.47	28.8	0.3–0.8	HNC
Harris´s Hawk	52	1.28	19.1	0.9–1.9	UC	16	1.62	37.8	0.8–3.4	HNC	68	1.28	18.1	0.9–1.8	HNC
Gray-backed Hawk	31	0.44	27.0	0.3–0.7	UC	9	0.54	51.2	0.2–1.4	HP	40	0.51	27.8	0.3–0.9	HNC
Short-tailed Hawk	12	0.17	31.1	0.1–0.3	UC	5	0.28	44.1	0.1–0.7	UC	17	0.16	25.1	0.1–0.3	UC
Zone-tailed Hawk	12	0.59	42.0	0.3–1.3	HNC	3	0.22	71.5	0.1–0.9	HNC	15	0.34	37.0	0.2–0.7	HP
Black Hawk-Eagle	13	0.18	25.0	0.1-0.3	UC	7	0.20	49.1	0.1–0.5	UC	20	0.19	23.5	0.1–0.3	UC
Laughing Falcon	35	0.49	18.2	0.4–0.7	UC	10	0.57	47.6	0.2–1.4	UC	45	0.42	17.5	0.3–0.6	UC
Crested Caracara	10	0.31	41.0	0.1–0.7	HP	7	1.11	61.1	0.4–3.4	HNHe	17	0.59	33.7	0.3-1.1	HNC
Bat Falcon	8	0.21	51.9	0.1-0.6	HNC	0	0	0	0		8	0.08	42.4	0.03–0.2	UC

Table 9. Raptor density estimates (D) in number of individuals km^{-2}, percentage of coefficient variation (CV) and 95% confidence interval (C.I.) of species using habitat types as a covariate in morning and afternoon evaluations pooled together.

	Dry Savanna			Dry deciduous			Deciduous			Semi-deciduous		
Species	D	CV	95% C.I.	D	CV	95% C.I.	D	CV	95% C.I.	D	CV	95% C.I.
Turkey Vulture	6.00	19.5	4.00-9.00	2.26	15.5	1.66-3.08	2.12	30.3	1.15-3.90	1.07	29.5	0.59-1.93
Black Vulture	3.80	35.2	1.84-7.85	1.43	18.1	1.00-2.04	1.30	26.7	0.76-2.23	1.20	35.7	0.57-2.40
King Vulture	0	0	0	0.42	35.7	0.21-0.83	0.35	61.4	0.11-1.12	0.77	34.8	0.39-1.54
Bicolored Hawk	N.A.			N.A.			N.A.			N.A.		
Crane Hawk	0.74	96.7	0.14-3.87	1.09	71.6	0.29-4.03	0.54	97.4	0.10-2.80	1.19	90.5	0.25-5.66

Savanna Hawk	N.A.			N.A.			N.A.			N.A.		
Great Black Hawk	0	0	0	0.53	41.9	0.24-1.19	0.48	39.5	0.22-1.05	0.52	36.4	0.25-5.66
Harris´s Hawk	2.23	26.7	1.29-3.88	2.12	23.4	1.33-3.36	1.28	44.5	0.53-3.07	0.55	50.4	0.21-1.47
Gray-backed Hawk	0	0	0	0.56	40.7	0.26-1.24	1.20	28.2	0.68-2.12	0.17	55.2	0.06-0.49
Short-tailed Hawk	0.16	70.1	0.04-0.59	0.19	52.7	0.07-0.51	0.17	57.2	0.06-0.51	0.32	39.6	0.15-0.70
Zone-tailed Hawk	0.18	102.6	0.03-1.08	0.43	50.7	0.17-1.13	1.05	49.1	0.41-2.70	0	0	0
Black Hawk-Eagle	0	0	0	0.04	70.8	0.01-0.15	0.19	41.9	0.08-0.44	0.55	24.6	0.34-0.90
Laughing Falcon	0.38	57.4	0.12-1.17	0.54	28.9	0.31-0.96	0.82	28.5	0.46-1.45	0.36	53.0	0.13-1.01
Crested Caracara	1.11	43.9	0.47-2.63	1.10	41.0	0.48-2.35	0	0	0	0	0	0
Bat Falcon	0	0	0	0.20	58.4	0.07-0.59	0.22	78.3	0.05-0.89	0	0	0

5.4.5 Raptor densities in different habitats

Density estimates for raptor species were calculated in four habitat types to identify habitat preferences per species based on habitat use. Number of detections were too low to estimate densities for Bicolored Hawk and Savanna Hawk per habitat types so were removed from analysis. All species were detected in dry deciduous forest and all but Crested Caracara in deciduous forest. Eight species were detected in dry savanna, ten in semi deciduous forest, and six in all four habitats. Absolute densities of Black and Turkey vultures were higher in dryer forests, while King Vulture had a higher density estimate in semi- deciduous forest and was absent from dry forest. The Harris´s Hawk and Crested Caracara showed a marked preference for dryer habitats, particularly of dry savanna. The Gray-backed Hawk, Zone-tailed Hawk, Laughing and Bat falcons showed preferences for dry deciduous and deciduous forest. Great-Black Hawk, and Black Hawk-Eagle were present in all habitats above 100 m. The eagle´s density increased in higher habitats while for the hawk it remained almost constant. There was a significant difference in the number of individuals per species detected in all four different habitats (Kruskall-Wallis Test $H = 8.88$, df = 3, $P = 0.03$; Table 9).

5.4.6 Population sizes for individual species

Of four habitats identified in the study area, dry forest was the smallest (41 km²) while deciduous forest was the largest (227.8 km²). All together, habitat types between 101 and 600 metres (dry deciduous and deciduous forests) accounted for 63% of all the study area and semi deciduous forest accounted for 30.3%.

Total population size of all 15 species of raptors combined was 5673 individuals; of these almost 70% were detected in dry deciduous and deciduous forest while only 11% were detected in dry savanna. Density of all raptor species per habitat type was higher in dry savanna (14 individuals km^{-2}) followed by dry deciduous (10.8 km^{-2}) and was lower in semi-deciduous habitat (6.7 km^{-2}).

The population size of Turkey and Black vultures accounted for 40% of the whole raptor population in the study area. In the Accipitridae, Harris´s Hawk had the largest population size (841 individuals). Of these, 77% occurred in dry deciduous and deciduous habitats between 100 and 600 m. With an estimated population of just 19 individuals, Bat Falcon had the lowest population of all species evaluated and almost all individuals were registered in dry deciduous forest. Individuals of the three species of Falconidae accounted for 11% of all raptors detected. Within this family, Laughing Falcon was the most abundant, particularly in dry deciduous and deciduous forest between 100 and 600 m. Population size of Gray-backed Hawk in the study area was 234 individuals. Of these, 86% occurred in dry deciduous and deciduous habitat. The Black Hawk-Eagle, a species that in west Peru is restricted to the northern part of the NWBR, had a population size of 154 individuals. Of these, 68% occurred in semi-deciduous forest above 600 m (Table 10).

Table 10. Population size (N) in number of individuals km^{-2} and 95% confidence interval (C.I.) of raptor species from transects counts pooled together (AM+PM).

	Dry Savanna		Dry deciduous		Deciduous		Semi-deciduous	
Species	N	95% C.I.	N	95% C.I.	N	95% C.I.	N	95% C.I.
Turkey Vulture	246	164-369	377	277-514	483	262-888	203	112-366
Black Vulture	156	75-322	239	167-340	296	173-508	227	108-455
King Vulture	0	0	70	35-138	80	25-255	146	74-292
Crane Hawk	30	6-159	182	48-672	123	23-638	225	47-1072
Great Black-Hawk	0	0	88	40-198	109	50-239	98	47-203
Harris´s Hawk	91	53-159	354	222-560	292	121-699	104	40-278
Gray-backed Hawk	0	0	93	43-207	109	50-239	32	11-93

Short-tailed Hawk	7	2-24	32	12-85	39	14-116	61	28-133
Zone-tailed Hawk	7	1-44	72	28-188	239	93-615	0	0
Black Hawk-Eagle	0	0	7	2-25	43	18-100	104	64-170
Laughing Falcon	16	9-48	90	52-160	187	105-330	68	25-191
Crested Caracara	46	19–108	183	80-392	0	0	0	0
Bat Falcon	0	0	17	5-52	2	1-23	0	0

5.4.7 Species detectability groupings

Figure 14 is a dendrogram showing clustering of 15 raptor species according to their detectability attributes. The analysis divided species into two main groups: The first comprised five species that were almost always detected flying (Table 7) and did not vocalize. Among these, the larger ones (Black Vulture, Turkey Vulture and King Vulture) were separated from the smaller ones (Zone-tailed Hawk and Short-tailed Hawk). The second main cluster included ten medium-sized to large species that were mostly detected perched. Species with very high percentages of individuals detected perched but with different degrees of conspicuousness (Bicolored Hawk, Laughing Falcon and Bat Falcon) were separated from those species that soared more often. These were separated in species that hunted from perches at mid to upper canopy (Harris´s Hawk, Great Black Hawk and Crane Hawk) or the ground (Savanna Hawk and Crested Caracara) with some species that vocalized during flight (Gray-backed Hawk and Black Hawk-Eagle) also set apart.

Pairs of species that were joined with cluster analysis were: Short-tailed Hawk with Zone-tailed Hawk, Bicolored Hawk with Bat Falcon, Gray-backed Hawk with Black Hawk-Eagle, Black Vulture with Turkey Vulture and King Vulture, Crested Caracara with Savanna Hawk and Harris´s Hawk with Great Black Hawk. Laughing Falcon and Crane Hawk were not included in the analysis because they were set apart from similar species and had enough detections themselves to obtain reliable density estimates. Density estimates obtained with the use of a multiplier for each species within a pair are presented in Table 11.

Figure 14: Dendrogram of raptor species grouped according to similarities in detectability.

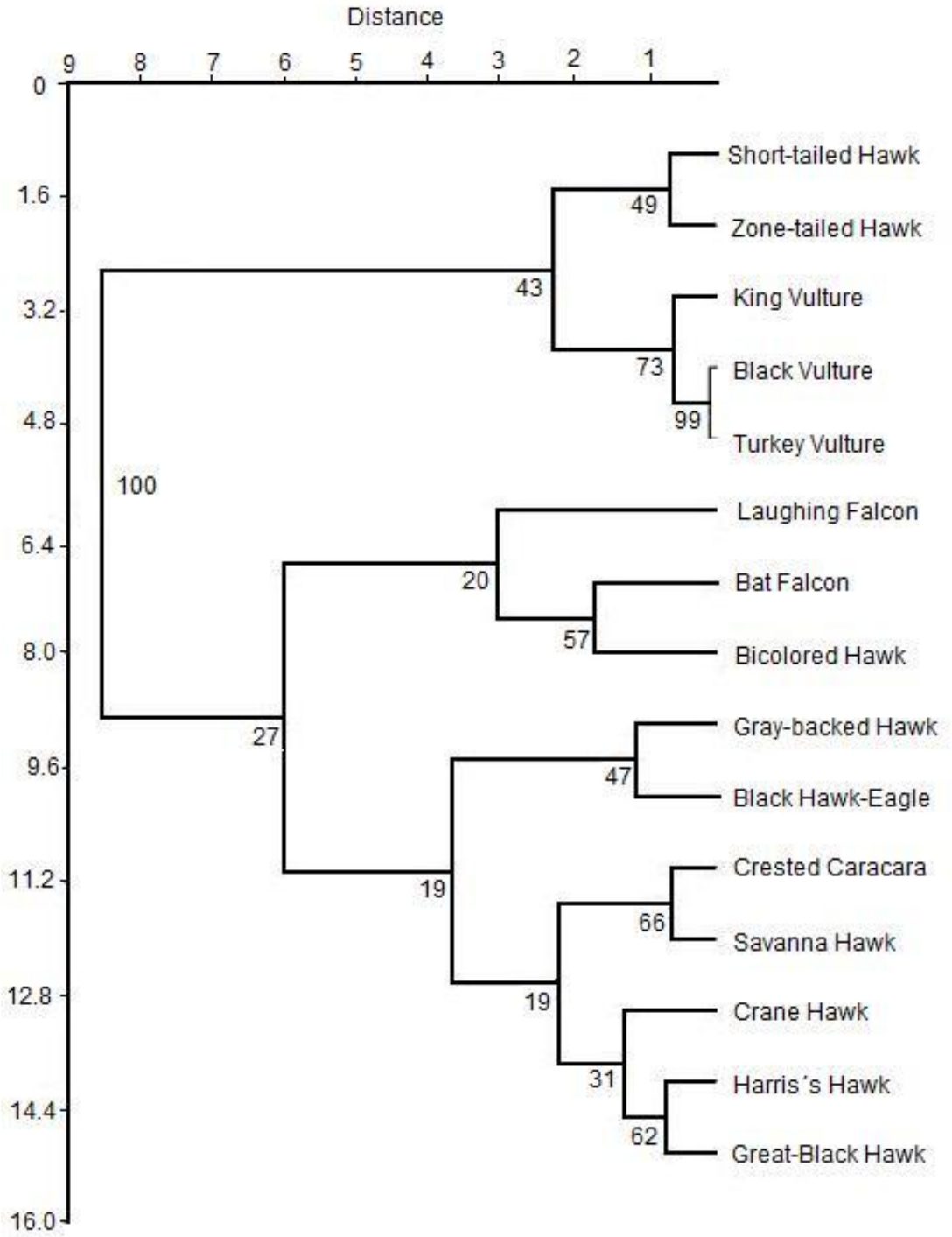

Table 11: Absolute density (D; individuals km^{-2}), percentage of coefficient of variation (CV) and 95% confidence interval (95% C.I.) of raptor species from morning and afternoon transects counts pooled together obtained with and without the use of multipliers.

	CDS			CDS with multiplier		
Species	D	CV	95% C.I.	D	CV	95% C.I.
Turkey Vulture	4.10	16.5	3.0-11.3	2.55	13.0	1.98-3.30
Black Vulture	1.72	18.1	1.2-2.5	2.04	16.5	1.47-2.81
King Vulture	0.36	27.4	0.2-0.6	0.47	23.8	0.30-0.75
Bicolored Hawk	0.13	43.9	0.1-0.3	0.07	46.4	0.05-0.17
Savanna Hawk	0.13	55.4	0.04-0.4	0.14	47.1	0.06-0.34
Great Black Hawk	0.47	28.8	0.3-0.8	0.52	25.1	0.32-0.84
Harris´s Hawk	1.28	18.1	0.9-1.8	1.21	17.3	0.86-1.70
Gray-backed Hawk	0.51	27.8	0.3-0.9	0.38	22.9	0.24-0.59
Short-tailed Hawk	0.16	25.1	0.1-0.3	0.29	27.0	0.17-0.49
Zone-tailed Hawk	0.34	37.0	0.2-0.7	0.26	32.1	0.14-0.48
Black Hawk-Eagle	0.19	23.5	0.1-0.3	0.19	23.5	0.12-0.30
Crested Caracara	0.59	33.7	0.3-1.1	0.48	32.8	0.06-0.34
Bat Falcon	0.08	42.4	0.03-0.2	0.08	46.8	0.03-0.19

Density estimates for six species (Turkey Vulture, Bicolored Hawk, Harris´s Hawk, Gray-backed Hawk, Zone-tailed Hawk and Crested Caracara) were reduced with the use of the multiplier, while for two species (Black Hawk-Eagle and Bat Falcon) remained the same. The highest variation with and without the multiplier in density estimate corresponded to the Short-tailed Hawk (81.3%), while the lowest was for Harris´s Hawk (5.4%). For eight species variation of density estimates was between 0 and 25%.

For species within a pair (or trio for the vultures), percentage of CV of density estimates for 'small hawks' (Bicolored Hawk and Bat Falcon) was increased, but for all vulture species, 'scrub hawks' (Crested Caracara and Savanna Hawk), and 'dark hawks' (Harris´s and Great Black hawks) it was reduced. Among 'soaring hawks' percentage of CV of density estimates for Short-tailed Hawk was increased but it was reduced for the Zone-tailed Hawk. For the 'vocal hawks', percentage of CV of density estimates for the Gray-backed Hawk diminished but for the Black Hawk-Eagle remained the same.

5.5 Discussion

5.5.1 Methods for estimating raptor densities

Absolute densities are necessary for determining population dynamics and effective population sizes of organisms, and are also key in helping to determine the level of threat facing a species (Franklin et al. 1990; Buckland et al. 2008). Despite the large volume of published literature on raptor counts (see Andersen 2007), few have ventured into calculating absolute density of raptor

species. Several methods are used to estimate raptor densities and these are usually conducted along routes or in fixed positions. Methods used are strip counts, point counts, spot-mapping and capture and marking (or recapture) of individuals (Fuller and Mosher 1987). Additionally, nearest-neighbour nest distance has been used to obtain densities of several species of raptors in temperate and tropical ecosystems (Newton 1976). Strip counts comprise several approaches that are used to calculate the density and/or abundance of objects by means of recording the distances from the objects to a line that is traversed by an observer (Emlen 1971; Thomas et al. 2010). In most of these approaches, the area of the strips where counts are performed should be known and all objects within the area need to be counted in order to obtain accurate measurements of density (Emlen 1971). Since detections beyond the strip boundaries are ignored, the use of these methods for wide ranging and usually scarce species (like raptors) are seriously questioned (Thomas et al. 2002). These methods are further complicated by several limitations that are related to observers' ability, weather conditions, variation in objects´ detectability, and conspicuousness of the objects that are counted (Emlen 1971; Fuller and Mosher 1987; Rosenstock et al. 2002).

5.5.1.1 Distance sampling methods

Distance sampling methods have been commonly used to calculate absolute densities of several bird taxa, but its use in raptors is still scarce (Boano and Toffoli 2002; Marsden and Pilgrim 2003; Shankar-Raman 2003). One key assumption of distance sampling is that all objects that are in the line of traverse

must be detected (Buckland et al. 1993; Bachler and Liechti 2007; Thomas et al. 2010). In a study conducted to evaluate the impact of vegetation structure on the detectability of various raptor models, Millsap and LeFranc (1988) found that the volume and distribution of foliage were the primary factors affecting detection of models, and that the use of counting methods that accounted for differences in detectability such as line transects improved accuracy of density estimates. However, they suggested that in most cases objects were not independent of the positions of transects because roads were used as transects. This has also been noted in Williams et al. (2000) when calculating densities of raptor species in different habitat types in Kansas, in Andersen et al. (1985) when calculating raptor population size in Colorado and in Boano and Toffoli (2002) when calculating densities of Common Buzzard (*Buteo buteo*) in northern Italy. In all these studies, roads were used as transects and given that roads are not placed randomly, raptor positions might have been influenced by the transect itself. Additionally telephone poles, a favored hunting perch for certain raptor species (Janes 1985) were present in some of these transects, influencing detectability of raptors and most probably, increasing density estimates.

In point transects, also referred as point count transects, evaluation points are positioned randomly and usually along a transect to ease access. Birds within a radius (fixed, variable or unlimited distance) from the centre of the evaluation point are recorded for a previously defined period of time and double counting of individuals is avoided. Priority is given to birds closer to the observer and assumptions are similar to those of line transects (Fuller and Mosher 1987; Thomas et al. 2002; Marsden and Pilgrim 2003; Thomas et al. 2010). Point

counts are preferred when evaluating difficult terrain and dense vegetation. It is also easier to relate bird density to habitat characteristics in a point than along a transect (Thomas et al. 2002; Buckland et al. 2008). There are however some shortcomings associated to point counts that might be particularly relevant when counting raptors: The effective counting period in point counts is relatively short (i.e. between to 6 to 20 minutes –Marsden and Pilgrim 2003; Lloyd 2008) and no counting is performed when moving from one point to another. Thus, line transects generate more detections given the same effort and this might be particularly relevant for species that occur at low numbers such as birds of prey (Buckland et al. 2008). However, Hall et al. (1997) used point counts along roads to calculate the density of the endangered Hawaiian Hawk (*Buteo solitarius*) and its relation with different habitat types while Klavitter and Marzluff (2007) used a combination of point counts with playback recordings to calculate Hawaiian Hawk density.

5.5.1.2 Spot-mapping

Spot-mapping is a method widely used to calculate densities of small bird species (Christman 1984; Terborgh et al. 1990; Kratter 1997) and has been used to a lesser extent with raptors because of their suspected large territorial requirements and because of their low rates of detection (Fuller and Mosher 1987; Terborgh et al. 1997). In spot-mapping, bird positions are plotted on a map and bird territories are determined from repeated visits to these same areas. Interaction with conspecifics by means of agonistic behavior or vocalizations help in defining territorial boundaries for individuals (Christman

1984). For a given species, the number of territories, the area of these territories and individuals contained within them are used to obtain the absolute density of the species. This method has been widely used to obtain densities of songbirds, yet several considerations regarding imperfect detectability (i.e. that detectability of individuals vary with distance from the observer and habitat types) have to be considered when using it (Terborgh et al. 1990; Kratter 1997).

Thiollay (1989) used a variation of spot-mapping to obtain data on numbers of individuals of 15 raptor species inhabiting 42 km² of forests in French Guiana. From an elevated point, he mapped the itinerary of individuals flying over the forest canopy. He also used conventional spot-mapping to determine home ranges of groups of Red-throated Caracara (*Ibycter americanus*) in this same area. The loud interactions between neighbouring groups helped to determine the limits of their territories. All other raptor species were detected too infrequently from the forest floor to accurately map their territories. Spot mapping was also used by Klavitter and Marzluff (2007) to calculate the absolute density of the Hawaiian Hawk. For this, all individuals in two study sites were captured and banded to ease identification. During surveys, broadcasting of the hawk´s calls was used to attract individuals to ensure that almost all individuals were detected.

5.5.1.3 Capture and marking

Capture and marking of individuals is used to estimate density of individuals along with other parameters such as productivity, recruitment, mortality rates, and reoccupancy of habitat (Gould and Fuller 1995; Kenward et al. 2000; Briggs

et al. 2011). This method involves the catching marking and releasing of individuals from a population. Then a sample size is taken and the number of marked individuals within the sample computed. An estimator of the population size is obtained by equating the proportion of marked individuals in the whole population to the proportion of marked individuals in the sample (Buckland et al. 2000). Since populations are not closed (i.e. there are births, deaths and immigration/emigration), researchers tend to use models, such as the Jolly-Seber that allow additions or deletions of individuals. This model renders accurate population size estimates providing that some assumptions are met: All individuals present in the sample have equal probabilities of capture, all marked individuals have the same probability of surviving, marks are not lost and all samples are instantaneous (Gould and Fuller 1985; Buckland et al. 2000). Capture and marking of individuals has been used to estimate the population size of Peregrine Falcons in Greenland (Gould and Fuller 1985) and population trends of Peregrines in the east coast and northern United States (Mueller et al. 1988; Prescott-Ward et al. 1988). However, estimation of raptors´ densities through mark-recapture can be subject to biases given that for some species survival and capture probabilities are age and sex dependant (Newton 1979; McFadzen and Marzluff 1996; Kenward et al. 1999). Also, capture and/or recapture probabilities might not be equal in raptors. During the breeding period individuals within a pair might not have the same probabilities of capture particularly when females spend more time in the nest and hunting and territorial defense is mostly performed by the male. Additionally, marked birds may be more likely to be resighted resulting in underestimation of population size (Gould and Fuller 1985; Manly et al. 1999).

5.5.1.4 Nearest-neighbour distance of nests

Nearest-neighbour distance of nests is used to determine the population of a species by counting the number of active nests within an area. Active nests are located either from vantage points or on foot and their location and the distance between nests can be easily obtained with a GPS. Inter-nest distance is used to estimate the number of nests that can be present in a larger area providing that habitat characteristics remain the same. A critical assumption is that nests in continuous habitat are roughly separated by a continuous distance and in a regular manner (Bueser et al. 2003), although it has been determined that for some raptor species inter-nest distances vary according to factors like soil fertility and vegetation composition and structure, and perhaps most importantly according to prey abundance and nesting site availability (Newton 1976; Newton 1979). The fact that some species build more than one nest in a breeding territory may complicate the calculation of species´ density through this method, so constant monitoring of suspected nesting sites should be carried out during research (Vargas-Gonzales and Vargas 2011). Additionally, there might be non-breeding individuals in addition to the breeding pairs in the study area so their numbers should be estimated considering the breeding success of the species and survival rates of the hatched individuals (Shultz 2002).

This method has been used to estimate population densities of species such as Crowned Eagle (*Stephanoaetus coronatus*) in Africa, Javan Hawk (*Spizaetus bartelsi*) in Indonesia, Phillipine Eagle (*Pithecophaga jefferyi*) in the island of Mindanao and to estimate the nesting density of Harpy Eagles in Panamá (van

Balen and Meyburg 1994; Shultz 2002; Bueser et al. 2003; Vargas-Gonzales and Vargas 2011). Additionally it has been used to estimate population densities of Peregrine Falcons in Spain (Heredia et al. 1988), and other parts of the world (see Cade et al. 1988). A different approach, based on the counts of individuals at nesting sites has also been used to calculate breeding densities of large falcons in North America and Greenland (Falk and Moller 1988; Olsen and Olsen 1988; Mossop and Hayes 1994; Shank and Poole 1994).

Few studies have attempted to calculate absolute density and population size of neotropical raptor species and studies based on rigorous sampling and analysis to calculate density estimates for neotropical raptor species within a community are particularly scarce. This is probably as a consequence of the inherent rarity (low density) in this avian group (Boano and Toffoli 2002). Minimum number of records detected for reliable density estimations has been set at around 100 (Buckland et al. 1993), although Andersen et al. (1985) used sample sizes equal or higher than 40 sightings to reliably define a detection function for raptors along line transects. Lloyd (2008) obtained density estimates for high Andean bird species with 20 or more records (although %CV of density estimates varied from 13.6 to 156.8). In this study, the number of individuals detected for only five species were higher or equal to 40, while for four species individuals detected were between 20 and 31. Despite this, %CV of density estimates (AM and PM transects pooled together) was below 30% for nine species and perhaps more importantly, I was able to obtain density estimates with good precision for six species with 17 to 31 detections. This is particularly relevant for researchers aiming to calculate demographic parameters of raptor species given that it is usually stated that intrinsic low numbers within the

Falconiformes prevents calculation of absolute density for most species (Fuller and Mosher 1987; Bibby et al. 1998; Millsap and LeFranc 1988; Williams et al. 2000; Boano and Toffoli 2002).

5.5.2 Encounter rate of raptors

Indices, such as encounter rates provide little and often problematic information on species abundance because they rest on critical and unrealistic assumptions concerning the detectability of target species (Anderson 2001). Despite their shortcomings, abundance indices such as raptor road counts are widely used to estimate raptor trends, community composition and habitat associations of species, including those of conservation concern, in temperate and tropical ecosystems (Williams et al. 2000; Thiollay and Rahman 2002; Ferguson 2004; Jensen et al. 2005; Andersen 2007; Simmons and Legra 2009). Road counts are favoured because they are relatively easy to implement (cars and roads are available almost everywhere), relatively inexpensive, and because vast areas of suspected raptorial habitat can be covered in a short time, counts from cars are suspected to yield more detections than counts performed by foot (Fuller and Mosher 1987; Millsap and LeFranc 1988). However, in most cases roads traverse across particular landscape features, avoiding steep or rugged terrain, flooded areas, etc. so is not possible to ensure that raptors are distributed randomly from the road itself. Relying on the availability of roads to perform raptor counts would leave vast areas within the tropics unexplored. Given the effect caused by roads and its impact on surrounding vegetation, habitat structure might be temporary or permanently affected at roadsides favoring detection of edge species at the expense of forest interior ones (Ellis et al.

1990) which in turn are the most vulnerable (Thiollay 1989b; Bierregard 1998; Bildstein et al. 1998) while evaluation speed is usually between 15 to 40 km h^{-1} (Fuller and Mosher 1987) seriously affecting detection of small species (Milsap and LeFranc 1988) and thus leaving them out from analysis.

The encounter rate of a given species might be influenced by its size. Species like the Black and Turkey vultures were among the larger, heavier, long winged species in the study area and had the highest encounter rates not only in account of their abundance but probably because of their higher detection probabilities derived from their larger size and behaviour. Large bodied and heavier species might be detected more easily particularly in open habitat as individuals are less able to remain concealed by vegetation (Millsap and LeFranc 1988). Additionally, vultures tend to perch on high exposed branches during the early morning hours, and soar during warmer periods thus favouring detection (Fuller and Mosher 1987). Highly vocal species like Harris´s Hawk, Laughing Falcon and Gray-backed Hawk had higher encounter rates than similarly sized but less vocal species such as the Crane, Short-tailed and Great-Black hawks. In contrast, small species such as the Bicolored Hawk and the Bat Falcon might have lower detection rates.

5.5.3 Raptor densities

This research is the first to use distance transect sampling to census diurnal raptors in Peru. The use of distance sampling methodologies to calculate raptor densities has been questioned because of suspected long periods of fieldwork in order to collect enough detections to perform analyses (Thiollay 1989b). In

this research however all detections were collected in 70 field days with a sampling effort of approximately five hours per day. The remaining time was mostly spent mapping trails inside the study area. Surveys were not conducted in the rainy season, and because raptors in the study area are suspected to breed with the onset of rains (Vargas 1995) density estimates were not affected by variation in species detectability derived from individuals attending nests. I acknowledge, however, that this might have changed over the study period as the months got drier and the trees lost their leaves.

In this research, I attempted to ensure that detection of all objects in the survey line was certain and that objects did not move away from the line with observer presence by evaluating transects at a relatively low speed (approximately 1 km h^{-1}), by making pauses to scan the vegetation close to the line and by focusing in detecting raptors on the transect (or close to it) or flying above the transect. Less attention was paid to flying or soaring individuals far away from the line because most certainly these records were to be removed from the analysis when visually inspecting detection functions and truncating outliers. Detection of individuals before evasive movement was maximized by wearing clothes with colours that helped reducing observers detectability and thus reducing the chances of raptors moving away from the transect prior to detection (Gutzwiller and Marcum 1997).

Percentages of flying birds for some species were very high (up to 100%), yet these individuals were included in calculation of absolute densities to increase sample size. Some species, namely Gray-backed Hawk and Black Hawk-Eagle performed aerial displays by means of flying in circles above transects; also all three vulture species and Short-tailed and Zone-tailed hawks frequently soared

in circles above the forest canopy. I calculated the centre of these circles during displays or soaring flights and then measured the distance from this point to the transect with a laser range finder. Although this might represent a violation of the distance assumption that that objects should be detected before natural or evasive movement from observer and thus might have inflated density estimates (Marsden 1999), most individuals were not flying away or towards the observer, allowing for accurate measurement of perpendicular distance from the centre of the bird position to the transect. Also, this approach is in line with the idea that distance sampling is a 'snapshot' method in which birds are 'frozen' in their initial positions. During surveys, flying birds moved independently of the observer's presence and thus bias was considerably reduced (Buckland et al. 2008). For some species (Short-tailed Hawk, Zone-tailed Hawk and King Vulture) encounter of perched birds is very rare, while others (Black Hawk-Eagle) are simply rare in the study area (Schulenberg et al. 2007) so I had to include individuals that were flying in circles and minimize the problem of movement to calculate their absolute density.

The inclusion of moving birds in absolute density estimates through Distance Sampling is not new. Censuses of flying birds through Distance Sampling along transects are widely conducted, particularly to estimate absolute density and population size of marine birds (Tasker et al. 1984), with some birds detected when performing avoidance movements (i.e. flying away from moving vessels where counts are performed) (Barbraud and Thiebot 2009; Buckland et al. 2012; Tasker et al. 1984).

I argue that absolute density estimates obtained by including flying birds detected while circling over the forest during transect evaluations is not a

serious violation of distance assumptions. This is because birds that were recorded during soaring flights along transects were almost stationary when they were flying in circles around a fixed point when detected and birds were also moving independently from the observer. This method is in accordance with the “snap-shot” approach to Distance sampling, as I “froze” the birds in their initial positions (Bibby et al. 1998; Buckland et al. 2008; Tasker et al. 1984), which was taken to be the centre of the circle made by the soaring bird.

Bird movements tend to be more problematic in point counts than in transect counts, because in the former the observer remain motionless during the counting period and birds that were not present in the plot enter it; it is also possible that birds that have been counted can leave and re enter the plot resulting in double counting of individuals (Buckland et al. 2008).

Although inclusion of flying birds might generate upward bias in density estimations (Buckland et al. 2008), I argue that double counting of raptor species in the study area was more problematic. However, the methodology I used for counting birds along transects minimized double counting given that transects were separated by at least 1 km from each other and none of them were evaluated simultaneously, thus eliminating the probability of recording the same flying bird from different transects. Double counting was also minimized by taking into account individual characteristics of soaring birds (e. g. plumage morph, age of birds, missing wing or tail feathers, etc.). Birds that were suspected to be previously detected were excluded from counts.

For species that were almost exclusively detected in flight (e. g. King Vulture, Turkey Vulture, Black Vulture, Zone-tailed Hawk, Short-tailed Hawk and Black

Hawk-Eagle), detection models with lower AIC values were obtained with Half Normal and Uniform key functions, and Cosine series expansions. The only exception was the Black Vulture. The Uniform key function performs well in a variety of situations while the Half Normal is selected when detection declines quickly with distance a feature that is expected in forested ecosystems like those present in the study area (Bibby et al. 1998).

During the surveys, other distance assumptions were met by randomly selecting all plots where survey transects were laid, and thus ensuring that all individuals were distributed randomly with respect to transect lines. Additionally, precise measures of perpendicular distance from objects to the transects was obtained with a range finder as suggested by Millsap and LeFranc (1988) and Rosenstock et al. (2002).

Absolute density of raptor species in the study area was significantly correlated with species encounter rates. However to obtain species encounter rate I included random encounters while traversing roads and trails in different habitats and at different times of day and did not account for differences in species detectability (Buckland et al. 2008). Some species (Savanna Hawk, Zone-tailed Hawk, Crested Caracara and Crane Hawk) showed low encounter rates compared to their densities, while for others (Bat Falcon, Black Hawk-Eagle and Short-tailed Hawk) the opposite was the case. Use of encounter rates for these species as a surrogate of their absolute density would have introduced serious biases in the estimation of their abundance and population sizes which in turn might have led to wrong inferences on their conservation status in extreme northwest Peru.

Absolute density of eagle species in Kenya was estimated in 2.38 individuals km^{-2} (Brown 1966), while in French Guiana´s rain forest absolute density of a diurnal raptor community was 4.44 individuals km^{-2} (Thiollay 1989b). Absolute density of all raptors in northwest Peru was extremely high (9.74 individuals km^{-2}) because of the high numbers of Black and Turkey vultures detected. When these two species were removed from analysis, the density estimate for raptor species was almost halved (5.46 individuals km^{-2}, %CV = 8.32%, 95% C.I. = 4.6-6.4). Absolute densities for Great-Black Hawk, King Vulture and Bicolored Hawk in northwest Peru were three to four times higher than those obtained for these species in French Guiana and for the Black Hawk-Eagle it was nine times higher (Thiollay 1989b), however density estimates obtained by Thiollay did not account for differences in detectability and thus might be biased. Density of the endemic Gray-backed Hawk was estimated to be 0.51 individuals km^{-2}, which is very much within the range of the density calculated for the species (0.5-0.6 individuals km^{-2}) by BirdLife International (2012). Although small study areas such as the one in this study tend to inflate density estimates because the increased probability of organisms moving across the area boundaries (Franklin et al. 1990), part of these differences can also be attributed to reduced detectability of rainforest raptors derived from variations in vegetation density, which may have affected detection of secretive and less conspicuous species, particularly of those favouring forest interiors.

Densities of Turkey and Black vultures were higher in drier habitats, which, in turn, were the most altered. It was here where all human settlements in and around the study area were located. These two species, but particularly Black Vulture, were frequently seen in high numbers around households, feeding on

refuse and carrion as has been observed elsewhere in their range (Lemon 1991; Rodriguez-Estrella and Brown 1990). Crested Caracara was also abundant at lower elevation habitat. This species was often encountered perched above or walking along river margins feeding on dead fish and frogs. Raptors are known to feed in areas where prey items are more easily accessed regardless of prey abundance (Preston 1990). Given the relative flat gradient at lower elevations in the study site, it is possible that Crested Caracara´s abundance was influenced by the increased number of beaches, estuaries and ponds at lower elevations, which, in turn, increased the species´ chances of finding food. Abundance of Black Hawk-Eagle increased at higher elevations where taller trees dominated the landscape. A long tail and short and rounded wings like those of the Black Hawk-Eagle enable raptors to maneuver in dense forest while heavier raptors with longer wings are more frequent in birds from open habitats (Mader 1978; Janes 1985). It is possible that in extreme northwest Peru, segregation of raptor species within the community is also related to the morphology of species and their ability to exploit particular features in the landscape as has been documented elsewhere (Janes 1985; Gammauf et al. 1998).

5.5.4 Improving density estimates of rare species

For nine species with detections ranging from 168 (Turkey Vulture) and 15 (Zone-tailed Hawk), %CV of absolute density estimates for species grouped with cluster analysis and calculated with the use of multipliers was lower than those obtained without grouping. For the Bicolored Hawk, the Bat Falcon and

the Short-tailed Hawk, %CV of absolute density estimates increased while for the Black Hawk-Eagle (20 detections) remained the same. It is possible that the number of detections for the Bicolored Hawk and the Bat Falcon (7 and 8 respectively) were too small to improve absolute density estimates, however for species with number of detections ranging from 20 to 40, the use of multipliers can improve their density estimates.

Results suggest that line transect distance sampling is a potentially useful method for assessing abundance for most raptor species that inhabit forested habitats in extreme northwest Peru. My analysis also shows that absolute density estimates for species can also be improved with the use of multipliers. In this study, exceptions were the Savanna Hawk, Bicolored Hawk and Bat Falcon. The Savanna Hawk is relatively common in shrubby habitat and agricultural fields outside the study area (Schulenberg et al. 2007), and given its abundance and conspicuousness elsewhere, might be very well suited for transects counts in preferred habitat. The Bicolored Hawk, a small and secretive species very difficult to detect (Thiollay 1989), and the Bat Falcon, another small species that is more active early in the morning or late in the afternoon might be more common in the study area than this research suggest. For the falcon, surveying at periods when the species is hunting might increase the detection of individuals, while for the hawk, broadcasting of conspecific vocalizations in points along transects to elicit individual responses (Fuller and Mosher 1996; Buckland et al. 2008) might be a better method to calculate absolute densities than transect evaluations. The lack of records of Collared Forest-Falcon and Barred Forest-Falcon during transects counts may well be a consequence of the time of day at which evaluations were performed. In order

to obtain absolute densities of these species, aural detections along transects like those conducted by Lloyd (2003) should be performed at dawn and dusk.

5.5.5 Conservation implications

The NWBR holds a highly diverse and particularly rich community of diurnal raptors that is unique in Peru (Piana 2011). Six species had absolute densities ranging from 0.59 to 4.14 individuals km^{-2} and for nine species it ranged from 0.08 to 0.51 individuals km^{-2}. According to Terborgh et al. (1990), large species with absolute densities of less than 0.5 individuals km^{-2} are particularly sensible to habitat degradation and might require large areas of intact habitat to maintain stable populations. For species like King Vulture, Black Hawk-Eagle, Great-Black Hawk, Short-tailed Hawk, Zone-tailed Hawk, Laughing Falcon, and Gray-backed Hawk, maintaining the integrity and continuity of forested areas in the CANP, the TNR and buffer zones might be vital for their survival in extreme northwest Peru. Further destruction of forests must be avoided while management of habitat mosaics outside the NWBR should also be enhanced to preserve as much forest cover as possible. The recently created Tutumo-Matapalo Regional Conservation Area, north of the CANP is a good step in this direction and should be replicated in adjacent Ecuador.

Habitat diversity is crucial to maintain species diversity within the diurnal raptor community in extreme northwest Peru given that most species showed a marked preference for particular habitats (i.e. only six species of the 15 included in this study were registered in all four habitat types). The endemic Gray-backed Hawk, the only endemic species in the study area (BirdLife International 2012)

was mainly detected in deciduous habitats at 100-600 m, and 64% of all sightings were between 200 and 500 m. In western Peru, the Black Hawk-Eagle is restricted to semi deciduous habitat in Tumbes and is also very scarce in western Ecuador (Ridgely and Greenfield 2001). My findings highlight the importance of these particular habitats for the species persistence in northwestern Peru, and west of the Andes in Peru and Ecuador.

Minimum viable population (MVP) has been defined as the number of individuals needed for a species to have a high probability of persistence in a given period of time (Shaffer 1981; Brook et al. 2006). For some species or taxonomic groups, MVP has been tentatively established between the higher hundreds and the lower thousands although most of these numbers are based more on theory than on observations of population dynamics (Thomas 1990; Brook et al. 2006). Walter (1990) showed that for the endemic Socorro subspecies of the Red-tailed Hawk (*Buteo jamaicensis socorroensis*) a population of approximately 50 individuals has been sufficient for the species to persist for at least 120 years in an island of 140 square kilometres (absolute density = 0.36 individuals km^{-2}). In the study area, population size of three species (Bat Falcon, Bicolored Hawk and Savanna Hawk) was lower than 19 individuals and are possibly too low to persist in the long term. However it may be that populations of Bicolored Hawk and Bat Falcon were underestimated due to the methods used to estimate them.

Apart from the Bat Falcon, population size of other five species, namely King Vulture, Great Black Hawk, Short-tailed Hawk, Black Hawk-Eagle and Crested Caracara were below 300 individuals and might be of higher conservation concern in the study area. Small populations in small habitat fragments have

high conservation potential providing that populations are not isolated (Thomas 1990). Maintenance of connectivity along the whole Tumbesian Centre of Endemism might provide higher probabilities of persistence during extended periods of time for these five species. Conservation of remaining patches along northwest Peru and western Ecuador might contribute in the creation of landscape corridors (Soulé and Simberloff 1986; Jones et al. 2012) that could help in maintaining connectivity between subpopulations of these species, and thus increasing their chances of survival in the Tumbesian Centre of Endemism.

Based on the density obtained from the entire study area, population size of the endemic and endangered Gray-backed Hawk was estimated at 319 (95% C.I. 187–563) individuals. However, since the species was absent from dry savanna, its real population size was estimated at 234 (95% C.I. 104–539). This is the first population size estimate obtained for the species in Peru. In Ecuador the current population size for this species has been calculated at 100–250 birds and the population is suspected to be declining due to ongoing habitat destruction and fragmentation (BirdLife International 2012). My results put into perspective the importance of the Peruvian population of Gray-backed Hawk and its habitat for the long term persistence of the species across its entire range. They also call for the urgent protection of remaining forested habitats within the NWBR in order to maintain its highly diverse raptor community.

Chapter 6: Influence of cattle grazing intensity on raptor distribution within a Peruvian protected area

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6.1 Abstract

Despite its impact on forest structure and biological diversity, cattle grazing is frequent in protected areas across the tropics. I used generalized additive models (GAMs) to examine the relationship between vegetation structure, elevation and cattle 'density' and raptor species richness metrics and the occurrence of six diurnal raptor species in 39 km² plots within the North West Biosphere Reserve, northwest Peru. Cattle grazing was widespread. Cattle density, estimated from transect counts of cow dung and corrected for accumulation rates was negatively correlated with average canopy height and percentage of vegetation cover from 5 to 15 m. Percentage of vegetation cover 5-15 m above the ground was the most important feature influencing richness of rare species and the distribution of four from six raptor species. Raptors responded differently to cattle density. Likelihood of presence of species that hunted or searched for food in open habitats increased with cattle density, while presence of range restricted or declining species decreased. The establishment of cattle pastures at the expense of standing forests may have detrimental impacts on the populations of range restricted species. Moderate cattle densities of approximately 60 individuals km^{-2} can be beneficial for some raptor species and might help to maintain the high raptor diversity in the study area, however, this activity should be monitored by NWBR authorities so no more forest is converted into cattle pastures.

6.2 Introduction

Creation of protected areas continues to be the main strategy to protect biological diversity (Ervin 2003; Hayes and Ostrom 2005; Naughton-Treves et al. 2006). However, in many tropical countries these are often weakly enforced by national and local authorities and activities that are detrimental for the maintenance of biological diversity are widespread inside parks and reserves (Peres and Terborgh 1995; Ervin 2003).

Free-range cattle grazing, an activity that allows unrestricted movement of cattle is widely conducted in tropical regions of the world (van Rees and Hutson 1983; de Haan et al. 1997), including protected areas (Naughton-Treves et al. 2006). Often, cattle are left to roam free in natural landscapes where they feed on the native vegetation (Stern et al. 2002). Additionally, natural areas are cleared to favour growth of native or introduced pastures that are beneficial for cattle. In the neotropics, cutting and burning of vegetation is a common practice to convert natural forest stands into homogeneous cattle pastures where few species predominate (Nepstad et al. 1999; Nepstad et al. 2001). This practice is known to affect species diversity given that grazed areas support a simplified array of wildlife and flora species and because structurally less complex vegetation provides habitat to fewer species (Roth 1976; Rotemberry and Wiens 1980; Stern et al. 2002; Krueper et al. 2003). Removal of vegetation by cattle causes changes in forest structure and composition that negatively affect diversity and community structure of plant and wildlife species, including those that are preferred prey of raptors (Stern et al. 2002; Torre et al. 2007; Johnson and Horn 2008). Soil compaction caused by cattle reduces the availability of

shelter for some species including rodents (Torre et al. 2007). However grazing opens up understory and this might benefit some raptors by increasing prey detectability and capture (e.g. Bechard 1982; Preston 1990).

Despite being reasonably well studied in temperate systems, little is known of the effects of cattle grazing on tropical raptors either across the wider landscape, or within tropical protected areas in particular. Knowledge of how communities and conservation-important species respond to grazing is important both to guide 'gross' protected area management policies (whether grazing should be permitted or not) and, ideally, inform on how raptors respond to different cattle densities/grazing pressures.

To this purpose, I use GAMs to identify the habitat features that best predict raptor species richness measures and the presence of individual species within the North West Biosphere Reserve. I was especially interested in how important cattle density was for raptors as compared to other habitat features. I then examined the shape of the response curves to estimated cattle density to identify any threshold levels at which species reactions are disproportionately positive or negative. The aims of this chapter were: 1. To use dung counts to obtain cattle densities in the study area and to relate it to the diversity, abundance and distribution of raptor species with the use of GAM. 2. To measure the impact of different levels of cattle density in the structure of the raptor community and in the distribution of single species in the study area. 3. To obtain thresholds levels of cattle density that can be used as gross management tools to maintain the highly diverse community of raptors that is characteristic of northwest Peru.

6.3 Methods

6.3.1 Raptor surveys

Thirty nine randomly chosen km^2 plots (1 km x 1 km) within a 25 x 25 km study area (6.2% of the total area selected) were surveyed during 2009. A small number of plots were too remote to allow safe access so plots up to 2 km closer to existing trails were substituted for these (Thiollay 1993). No two plots were chosen if they fell in adjacent squares. All diurnal raptors seen or heard perched or flying along each transect were recorded and their distance to the transect line was measured with a range finder. See Raptor surveys and habitat recordings for more details in the methodology used.

6.3.2 Habitat data collection

Habitat measurements were taken at eight points located 200 m apart along each transect. To avoid possible biases derived from sampling along edges, evaluations were conducted 15 m perpendicular to the trail inside the forest. Elevation, latitude and longitude were recorded with a GPS, gradient was measured with a clinometer, canopy height was visually estimated, and percentage cover at different three vegetation strata (1-5 m, 5-15 m, and 15-25 m above ground) were estimated and then averaged within each transect.

Total number of stems from 0.1 to 2 cm diameter (1 metre above ground) were counted on four 2 x 2 m square plot located inside each of the strips where cattle dungs were counted (Figure 15). The centre of the plot was laid at the midpoint of the strip, 7.5 m away from the point where the above habitat variables were recorded. Number of stems was averaged across the 4 m^2 plots.

6.3.3 Cattle density estimation

Dung counts have been widely used as an indirect method to obtain abundance estimates of terrestrial vertebrates (e.g. Plumptre 2000; Palmer and Truscott 2003). The method gives accurate density estimates providing that defecation rates and dung decay are incorporated in calculations of final abundance numbers and standard sampling methods are used to lay sampling units in the field (Bailey and Putman 1981; Barnes 2001; Marques et al. 2001).

All cattle dungs were counted in four strip transects fifteen metres long and two metres wide (Figure 15; total area = 120 m^2), and this figure expressed as number of dungs km^{-2}. Given the abundance of rains during the wet season in the study area, number of cow dungs in the field were assumed to fall to zero at the end of the rains (taken to be 31 March in the year of study). While there is clearly no immediate 'switching off' of the rains at the onset of the dry season, it was assumed that cattle dungs were accumulated in areas at a given rate per day, with no destruction of cattle dungs during the dry season. This lack of heavy rain during the dry season meant that cow dungs simply dessicated where they were dropped. To estimate cattle 'density' within plots, number of total cattle dungs was corrected by incorporating the number of days between the end of the rains and the date on which each plot was surveyed. There was a near positive significant correlation between density of cattle dungs and number of days after the rainy season ended (r_s = +0.30; P = 0.06; Figure 16).

Figure 15. Stem and cow dung evaluation plot layout in relation to main habitat and raptor survey transect.

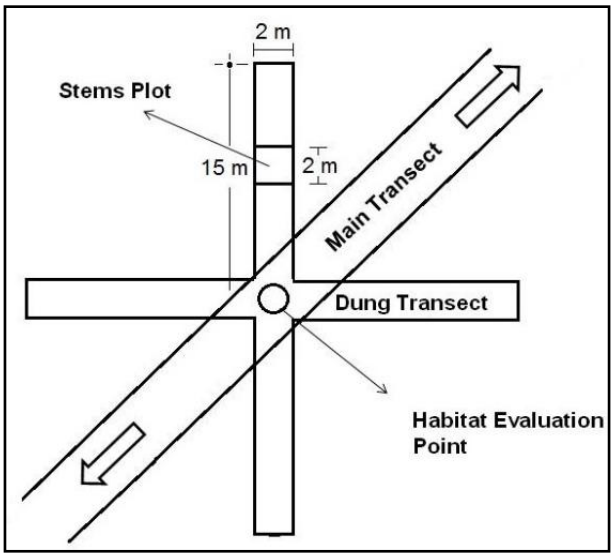
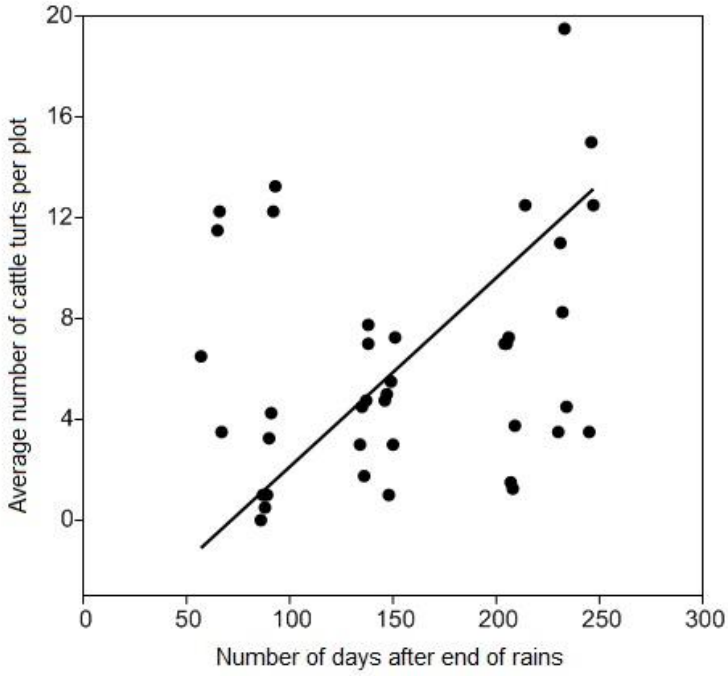


Figure 16: Scatterplot of mean number of cattle dungs counted per plot and number of days after the end of rain season.



From a literature search of dung production rates (Table 12), daily production of cattle dungs per cattle individuals was estimated to be 13. Cattle density in a plot was calculated by dividing the total number of cattle dungs per square kilometre in that plot by the number of days between the end of the rains and the date of evaluation multiplied by dung production rate.

Table 12: Mean cattle dung production rate ± standard error (SE) or standard deviation (SD) and sample size (n) in different habitats/regions from published sources (Reference).

Country/habitat	Mean	SE	SD	n	Reference
New Zealand/north	10.5	0.31	1.32	18	Weeda (1967)
Kenya/Arid savanna	13.0	0.44	-	7	Augustine (2003)
Belgium/coast	14.4	-	-	-	Cosyn et al. (2005)
New Zealand/south	13	-	-	-	McDowell (2006)
Japan/south	13.6	0.48	3.32	23	Hirata et al. (2009)
Switzerland/alpine	12.5	2.5	3.53	-	Gillet et al. (2010)

6.3.4 Raptor response variables

The most common species were found in almost all plots (Turkey Vulture and Black Vulture were found in 30 and 26 plots respectively), while the less

common (Bicolored Hawk, Crane Hawk, Zone-tailed Hawk, Crested Caracara and Bat Falcon) were detected in three to six plots. GAMs do not perform well with small sample sizes (Wisz et al. 2008) so I restricted habitat association analyses to more common species with 9 or more records. These were King Vulture (recorded in 14 km^2 plots), Gray-backed Hawk (12 plots), Great Black Hawk (12 plots), Black Hawk-Eagle (17 plots), Harris´s Hawk (20 plots), and Short-tailed Hawk (9 plots).

Along with the presence/absence of individual species, I included the following three composite measures of raptor diversity/abundance. Species richness was the number of species of any raptor (not just the six included above) recorded within the plot. I calculated the Shannon-Wiener diversity index for each plot, and an index of rarity for each plot as follows. For each species recorded within the plot I multiplied the number of records within the plot by the inverse of the population density at which it was estimated to occur within the study area. Density estimates were derived using line transect distance sampling in 70 km^2 plots randomly selected from across the study area. Density estimates (see Table 8) were calculated from species-specific detection functions in the Conventional Distance Sampling (CDS) engine of DISTANCE 6.0 (Thomas et al. 2009). See absolute densities in Chapter 5.

6.3.5 Autocorrelation and variable selection

The predictor variables were tested for autocorrelation through Spearman´s rank correlation tests in PAST software (Hammer et al. 2001). Pairs of variables with alpha values less than 0.05 were considered significantly correlated so one

variable (the one thought to be less influential for raptor distribution) was removed from analysis (Lor and Malecki 2006). Number of stems, elevation, latitude and longitude were significantly correlated with percentage of vegetation cover from 15 to 25 m above ground ($P < 0.05$). Gradient was significantly correlated with elevation ($r_s = +0.41$; $P < 0.01$). The index of cattle density was negatively correlated (albeit weakly) with a number of vegetation measures: with number of stems ($r_s = -0.3$; $P < 0.05$), average canopy height ($r_s = -0.40$; $P < 0.01$), and percentage of vegetation cover 1-5 m above ground ($r_s = -0.22$; $P = 0.18$). Based on these analyses, the following variables were selected as predictors for the GAMs: elevation (elev), average canopy height (can); percentage of vegetation cover 5-15 metres above ground (cov5); number of stems (stems); and number of cows per km² (cows).

6.3.6 Raptor-habitat association models

Generalized Additive Models are extensions of Generalized Linear Models (GLMs) that replace the linear regression coefficients with semi-parametric smoothing functions and additively calculate the component response (Hastie and Tibirishani 1986; Guisan et al. 2002; Heinanen et al. 2008). GAMs allows for the probability distribution of the response variable and the link between predictors and the probability distribution to be more general and are better suited to deal with highly non-linear and complex relationships between the response and predictive variables predictors (Granadeiro et al. 2004; Vilchis et al. 2006).

I ran logistic GAMs for the presence/absence of six raptor species and Poisson GAMs for the diversity/rarity indices using the 'mgcv' package in R (R Development Core Team 2012) version 2.15.0. Model selection was based on minimising Akaike´s Information Criterion (AIC) (Burnham and Anderson 2002). AIC 'measures' how good a particular model explains deviance in the data but penalizes models with a large number of parameters (Johnson and Omland 2004). All models within less than four AIC points compared with the model with the lowest AIC value were considered as competing models and selected for analysis (Pedrana et al. 2008). Akaike Weights (Wi) were used as a measure of the probability that a model have for being the best among the whole set of candidate models (Burnham and Anderson 2002; Johnson and Omland 2004).

6.4 Results

6.4.1 Cattle presence and density

Cattle dungs were recorded in all but one of the 39 plots. Cattle densities were calculated to average 29.2 individuals km^{-2} ± 28.9 (SD) in plots. There were no significant differences in cattle 'densities' between habitat types (dry savanna forest; dry deciduous forest and semi-deciduous forest: Kruskal-Wallis Test H = 3.07, df = 3, P = 0.38), nor were there significant differences between the three different protected areas regimes (Tumbes Reserve; Cerros de Amotape National Park; buffer zones: Kruskal-Wallis Test H = 5.03, df = 2, P = 0.08). Additionally, there was no significant correlation between cattle density and the average distance from plots to the three main cattle ranching towns in the study

area: Pampas de Hospital, Tutumo and Peña Blanca (r_s = -0.13; P = 0.44) nor with gradient (r_s = -0.13; P = 0.43).

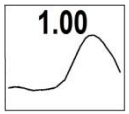
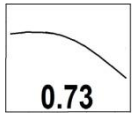
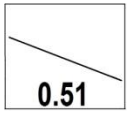
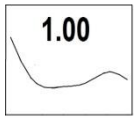
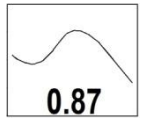
6.4.2 Raptor-habitat models

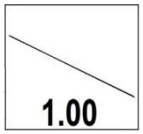
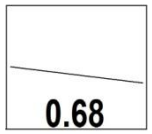
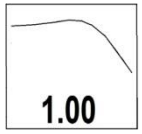
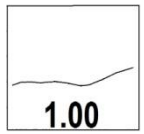
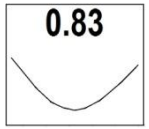
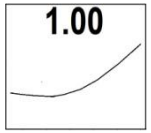
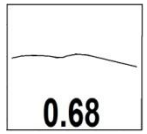
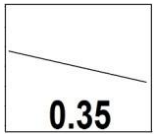
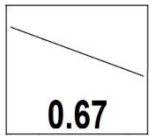
Best models are shown in Table 13 and full sets of models are shown in Appendix 1. Percentage of vegetation cover 5-15 m (cov5) appeared in seven of all best models selected, while remaining variables appeared in five or less. Richness was most likely influenced by elevation, number of stems and vegetation cover 5-15 m, while presence of rarer species was influenced by vegetation cover 5-15 m, cattle density and number of stems. Shannon index values were influenced by elevation. There was a strong relationship between the presence of Black Hawk-Eagle and elevation and between the presence of Short-tailed Hawk and percentage of vegetation cover 5-15 m so these variables were not included when building models for these two species (Guisan & Thuiller 2005). Overall, percentage cover 5-15 m was likely to appear in best models for most if not all raptor species (Table 13 and 14) and was probably the most powerful habitat variable that influenced raptor distribution.

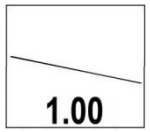
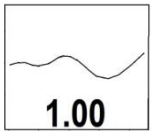
Table 13. Best model selected (∆AIC = 0) for each response variable evaluated.

Response Variable	Predictive variables
Richness	elev stems cov5
Shannon index	elev
Rarity	cov5 stems cows
Gray-backed Hawk	can cov5
Great Black Hawk	elev can cov5
Black Hawk-Eagle	cov5 stems
Harris's Hawk	elev can cov5 cows
Short-tailed Hawk	elev can
King Vulture	can cov5 stems cows

Table 14. Summary of Generalised Additive Models (GAM) for raptor species in extreme northwest Peru. Values given are the sum of Akaike weights for each variable. * Variables not included in GAM.

	Elevation	Canopy	%5-15m	Stems	Cows
Richness	0.64	0.40			0.26
Shannon		0.32		0.32	0.30
Rarity measure	0.39	0.48		0.81	

Great Black Hawk				0.46	0.49
Harris's Hawk				0.00	
Gray-backed Hawk	0.35			0.39	0.58
Black Hawk-Eagle	*	0.24			0.39
Short-tailed Hawk		0.30	*		0.33

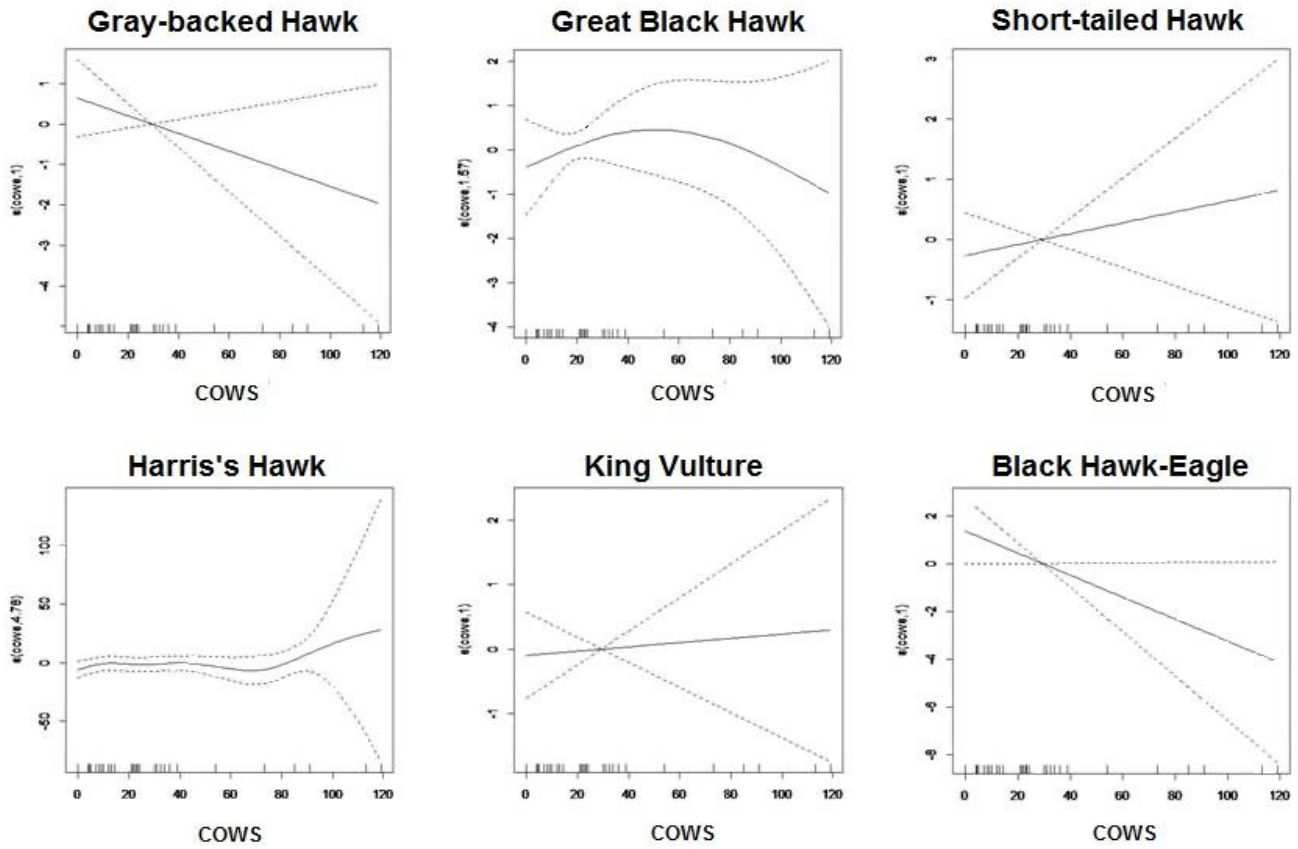
King Vulture	0.00				

6.4.3 Influence of cattle density

Individual species responded differently to increasing cow densities (Figure 17a). Gray-backed Hawk and Black Hawk-Eagle presence decreased linearly with increasing cattle density, while the opposite occurred for Short-tailed Hawk and King Vulture. Presence of Great Black Hawk also increased with increasing cattle density but then diminished at a density of approximately 50 cows km^{-2}. Harris´s Hawk presence remained constant at increasing levels of cattle density but increased at densities around 80 cows km^{-2} (Figure 17a). Species richness increased almost linearly with increasing cattle density, while species richness and the relative abundance of each species, expressed as the value of the Shannon-Wiener Index decreased. The index of rarity increased as cattle density increased from 20 cows km^{-2} to 60 cows km^{-2} but beyond this density, it declined (Figure 17b).

Figure 17: Partial GAM plots for A. presence-absence models for individual raptor species, and B. raptor richness/rarity measures, with cattle density as the predictor variable. Cattle density (individuals km^{-2}) is shown on the X axis. The dotted lines represent the 95% confidence interval around the response curve.

A.



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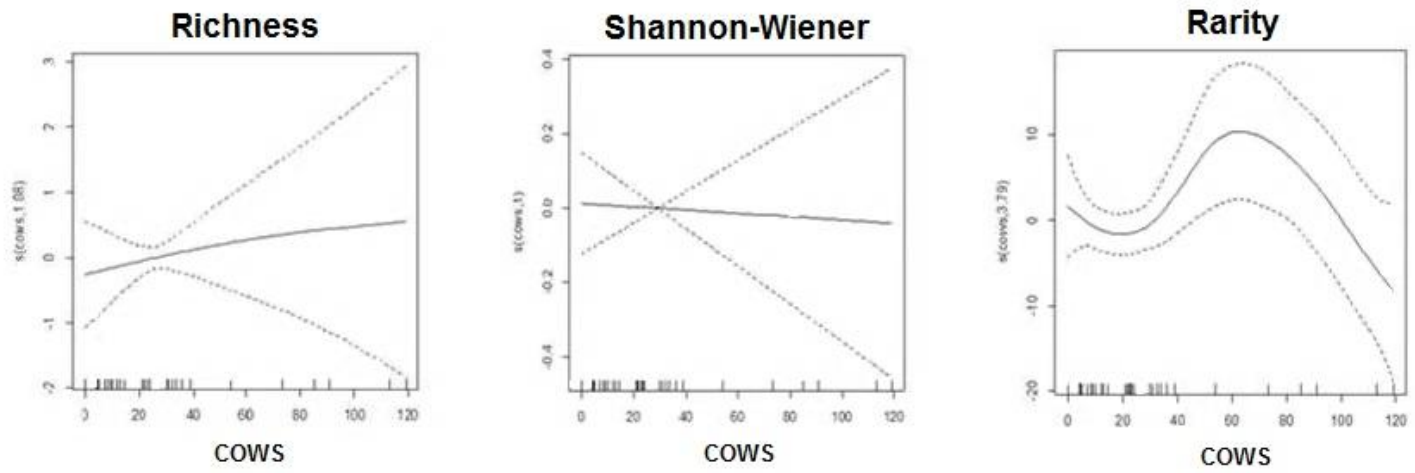
B.



6.5 Discussion

Despite available evidence of its impact on vegetation (Schulz and Leininger 1990; van de Koppel, 1997; Stern et al. 2002), cattle grazing is widely conducted in protected areas within neotropical dry forests (Guerrero 2002; Naughton-Treves et al. 2006) and the NWBR is no exception (Leal-Pinedo and Linares-Palomino 2005). In my study area, almost every area showed evidence of cattle presence. Cattle grazing in forests can change the structure and composition of vegetation in many ways: Cattle feed on forest understory altering forest structure, reducing density of lower strata, and changing plant species composition (Schulz and Leininger 1990; Krueper et al. 2003; Kutt and Woinarski 2007; Torre et al. 2007).

Whilst the focus of this study was cattle grazing, the findings point to an importance for raptors of vegetation structure in the upper strata which is presumably not directly related to the activities of cattle. For species such as Gray-backed, Great Black, and Harris´s hawks and Black Hawk-Eagles, vegetation and cover in the upper strata might influence the availability of perching sites, or can provide concealment to avoid predation for adult and young birds (Marion and Ryder 1975; Titus and Mosher 1981; Bohall and Collopy 1984; Preston 1990). Falconiformes also benefit from the presence of prey species that are more active in the forest canopy (Bednarz 1988; DeStefano and McCloskey 1997; Miranda et al. 2006). Additionally, nests described for the species included in this study are stick structures constructed

high above ground and concealed within the tree canopy (Mader 1978; Rangel-Salazar and Enriquez-Rocha 1993; Vargas 1995, Seavy and Gerhardt 1998).

In this study, raptors responded differently to cattle density. Presence of Black Hawk-Eagle, a forest species, declined linearly with increasing cattle density, as did Gray-backed Hawk, a border species that mostly prey on snakes (Vargas 1995) in a fairly wide range of habitats (Piana and Marsden 2012). Trampling and reduction of forest understory by ungulates, including cattle, is a major cause of bird declines in grazed areas (Fuller 2001), and influences the abundance of terrestrial vertebrates such as amphibians, reptiles and rodents (e.g. Kutt and Woinarski 2007; Cano and Leynaud 2009) which rank highly in diet composition of most of the raptors studied here. The reactions of two other species were more complex. Great Black Hawk had highest probability of presence when cattle density was close to 60 individuals km^{-2} while the edge-associated Harris´s Hawk (GRIN 2012) appears to prefer areas where cattle density exceeded 80 individuals km^{-2}. It is interesting to note that, although it is an almost obligatory carrion feeder that prefers medium sized to large carcasses (Robinson 1984; Schlee 2005), King Vulture showed little association with increasing cattle density. Short-tailed hawks, a species which mainly hunts birds, mammals and reptiles by soaring above open woodland, woodland edges and savanna type habitats (Odgen 1974; GRIN 2012) were associated with higher cattle densities. This species may benefit from increased densities of reptiles in recently cleared pastures or in degraded/recently burnt woodlands (e.g. Letnic et al. 2004; Cano and Leynaud 2009), or equally may be able to

more easily detect and catch ground-dwelling birds and mammals in open spaces (Preston 1990).

Richness and Shannon-Wiener index responded differently to increasing values of cattle density. Species richness within plots increased non-linearly with increasing cattle density. In the study area, areas used for cattle grazing are cleared for the establishment of pastures at the expense of standing forest, so increased number of species in areas with more cattle could be a consequence of the increased presence of edge species that, in the raptor community of extreme northwest Peru, are more abundant (Piana and Marsden 2012). Decreasing values of Shannon-Wiener index with increased values of cattle density reflects, I believe, the increasing dominance of the raptor community by species such as Harris's Hawk, and Black and Turkey Vulture in areas of higher grazing pressure. Similar dominance under high grazing pressure has been found in a number of taxa (e.g. Knopf et al. 1988; Saab and Petit 1992; Smith et al. 1996; Cano & Leynaud 2010).

Of particular concern was the negative effect of grazing on two important raptor species. Black Hawk-Eagle is restricted to semi-deciduous forests above 600 m (Piana and Marsden 2012), where its presence in the Tumbesian Centre of Endemism is seriously threatened by forest conversion and fragmentation (Ridgely and Greenfield 2001). The threatened Gray-backed Hawk, despite being relatively tolerant of forest alteration, has a rapidly declining population due to continuous habitat destruction for the establishment of pasturelands for cattle grazing (BirdLife International 2012). While strict control of grazing

(ideally, its cessation) would benefit these species, the index of raptor species abundance, weighted according to rarity, showed a non-linear response to grazing pressure. Generally across the community, grazing at cattle densities of 20-50 individuals km^{-2} actually benefited the raptor community suggesting that tolerance of cattle in some areas is appropriate. Abundance of rare raptor species decreased steadily at densities beyond 60 cows km^{-2} and such cattle densities should be used as a threshold level by protected area managers to maintain 'healthy' raptor communities in natural protected areas like the Tumbes National Reserve where cattle grazing is permitted.

Dung counts have been used to estimate density of large mammals in different forested environments in the tropics providing that defecation rate of target animals is calculated and decay rate of droppings is accounted (Plumptre and Harris 1995; Plumptre 2000; Marques et al. 2001). During this research cattle density was easily calculated by counting cow dungs along defined short strips on every plot. This method allowed to rapidly count cattle dung while covering large areas during raptor censuses. In my study area rains are highly seasonal. Yearly average precipitation at El Caucho research station is approximately 950 mm and 90% of this occurs between January and March (Nunez and Zegarra 2006). For this, I assumed that no cattle dung from previous seasons remained in the field after the end of rains. Additionally, no rains occurred during surveys so dung decay rates were considered null as they desiccated as the dry season progressed. No dung beetles were observed during dung counts. Dung production rates of cattle were obtained from literature search from research

mostly conducted in temperate areas. Given that digestibility of tropical forage is generally lower than that for temperate forage (Buschbacher 1997), it is possible that average dung production rate by cattle in my study site was lower than that assumed for density calculations. If this assumption holds, then cattle density in plots could be higher than this study shows.

Analysis of the impact of cattle grazing in animal communities has shown that these tend to be dominated by generalist species after vegetation composition and structure is modified by cattle. In northeast Argentina, Cano and Leynaud (2010) detected changes in abundance of lizard species and in the composition of the lizard community at cattle densities close to 30 cows km^{-2}, while in arid grasslands of southern Australia the rodent community in more heavily graced areas tended to be dominated by the introduced common mouse (*Mus musculus*; Read and Cunningham 2010). Presence of some generalist raptor species in my study site also increased with increased cattle density. The Harris's Hawk, a species of arid scrub and savanna that do well in disturbed areas (Rodriguez-Estrella et al. 1998; GRIN 2012) increased at cattle densities of 80 individuals km^{-2} while Great Black Hawk, species that is more associated to forests (GRIN 2012) declined at densities of 60 individuals km^{-2}. Increased cattle grazing in the NWBR can lead to a simplification of the raptor community. Given that the density of cattle permitted in certain parts of the TNR is 127 cows km^{-2} (SERNANP 2010), this amount should be halved to help maintain less generalist raptor species in the reserve.

Appendix 1. AIC scores for all GAMS predicting a) Shannon Index, b) species richness, c) presence of rare species, d) presence of Gray-backed Hawk, e) presence of Great Black Hawk, f) presence of Black Hawk-Eagle, g) presence of Short-tailed Hawk, h) presence of King Vulture. Asterisks denote the variables included in models.

Species richness

Elevation	Density of cows	%cov5-15	No. of stems	Canopy	AIC	ΔAIC
+		+	+		161.73	0
+		+	+	+	163.40	1.67
+	+	+	+		163.51	1.78
				+	163.55	1.82
		+	+		163.71	1.98
	+	+	+		164.35	2.62
+			+	+	164.58	2.85
+			+		165.22	3.49
+	+	+	+	+	165.40	3.67
	+			+	165.52	3.79
		+	+	+	165.66	3.93

	+	+	+	+	165.92	4.19
+	+		+	+	166.55	4.82
+	+		+		167.09	5.36
+		+			167.29	5.56
		+			168.52	6.79
+		+		+	168.54	6.81
+	+	+			169.00	7.27
+				+	169.22	7.49
		+		+	169.89	8.16
		+			170.06	8.33
+	+	+		+	170.07	8.34
+	+			+	170.16	8.43
		+		+	170.25	8.52
	+	+			170.44	8.71
	+		+	+	170.57	8.84
	+		+		170.73	9.00
	+	+		+	172.15	10.42
+					172.38	10.65
+	+				174.37	12.64

	+				180.28	18.55

a) Shannon Index

Elevation	Density of cows	%cov5-15	No. of stems	Canopy	AIC	ΔAIC
+					42.68	0
+	+				43.59	0.91
+		+			43.61	0.93
+			+		43.84	1.16
		+			44.22	1.16
+	+	+			44.29	1.61
		+		+	44.37	1.69
+				+	44.58	1.90
+		+		+	44.74	2.06
+	+		+		44.98	2.30
+		+	+		45.03	2.35
			+		45.40	2.72
		+	+		45.49	2.81

+	+			+	45.50	2.82
+			+	+	45.75	3.07
		+	+	+	45.92	3.24
+	+	+	+		45.94	3.26
	+	+			46.07	3.39
+	+	+		+	46.10	3.42
+		+	+	+	46.31	3.63
	+	+		+	46.37	3.69
				+	46.56	3.88
	+				46.58	3.90
+	+		+	+	46.91	4.30
			+	+	47.36	4.68
	+		+		47.39	4.71
	+	+	+		47.41	4.73
+	+	+	+	+	47.78	5.10
	+	+	+	+	47.92	5.24
	+			+	48.54	5.86
	+		+	+	49.35	6.67

b) Rarity

Elevation	Density of cows	%cov5-15	No. of stems	Canopy	AIC	ΔAIC
	+	+	+		259.84	0
	+	+	+	+	260.37	0.53
+	+	+	+		260.73	0.89
	+	+		+	261.61	1.77
+	+	+	+	+	262.11	2.27
		+	+		263.04	3.20
+		+	+		263.10	3.26
+	+	+		+	263.20	3.36
+		+		+	263.78	3.94
+		+	+	+	264.22	4.38
		+	+	+	264.45	4.61
	+	+			264.99	5.15
+	+	+			265.57	5.73
+		+			266.65	6.81

		+			267.14	7.30
	+				268.61	8.77
	+		+		269.46	9.61
+	+				270.00	10.16
+			+	+	271.03	11.19
+	+		+		271.13	11.29
			+		271.51	11.67
+	+			+	271.93	12.09
+			+		272.58	12.74
+	+		+	+	272.99	13.15
			+	+	273.34	13.50
+					273.41	13.57
				+	274.40	14.56
	+		+	+	274.47	14.63
+				+	275.31	15.47

c) Presence of Gray-backed Hawk

Elevation	Density of cows	%cov5-15	No. of stems	Canopy	AIC	ΔAIC
		+		+	44.35	0
	+	+		+	44.78	0.43
	+		+	+	45.13	0.78
+		+		+	45.27	0.90
+	+	+		+	45.95	1.60
	+	+	+	+	46.08	1.73
		+	+	+	46.18	1.83
	+	+			46.78	2.43
+	+		+	+	46.99	2.64
+		+	+	+	47.12	2.77
+	+	+	+	+	47.48	3.13
		+			47.97	3.62
+	+	+			47.98	3.63
	+	+	+		48.77	4.42

				+	+	49.49	5.14
+				+	+	49.55	5.20
+					+	49.79	5.44
			+	+		49.85	5.50
+	+		+	+		49.90	5.55
					+	49.93	5.58
+			+			49.94	5.59
	+				+	50.40	6.05
+	+				+	51.11	6.76
	+			+		51.60	7.25
+	+					51.67	7.32
+			+	+		52.39	8.04
+	+			+		52.39	8.04
	+					52.52	8.17
+						52.91	8.56
+				+		53.82	9,47
				+		53.87	9.52

d) Presence of Great Black Hawk

Elevation	Density of cows	%cov5-15	No. of stems	Canopy	AIC	ΔAIC
+		+		+	35.92	0
+	+	+		+	36.00	0.08
+	+	+	+	+	36.35	0.43
+		+	+	+	37.57	1.65
		+	+	+	37.75	1.83
		+		+	38.07	2.15
	+	+	+	+	38.45	2.51
	+	+		+	40.01	4.09
			+	+	48.12	12.20
				+	48.36	12.44
	+			+	49.81	13.89
+		+	+		49.82	13.90
			+		49.86	13.94
	+		+	+	50.01	14.09

		+	+		50.12	14.20
		+			50.27	14.35
+				+	50.32	14.40
+	+		+	+	50.79	14.87
+		+			51.31	15.39
+			+		51.37	15.45
	+				51.54	15.62
+			+	+	51.67	15.75
+					51.70	15.78
	+	+	+		51.75	15.83
+	+	+	+		51.77	15.85
	+		+		51.82	15.90
	+	+			51.97	16.05
+	+			+	53.10	17.18
+	+	+			53.10	17.18
+	+				53.17	17.25
+	+		+		53.34	17.42

e) Presence of Black Hawk-Eagle

Elevation	Density of cows	%cov5-15	No. of stems	Canopy	AIC	ΔAIC
		+	+		41.88	0
	+	+			43.23	1.35
		+	+	+	43.86	1.98
	+	+		+	45.20	3.32
	+	+	+		45.23	3.35
	+	+	+	+	46.99	5.11
	+				50.08	8.20
	+		+		51.15	9.27
		+			51.57	9.69
	+			+	52.00	10.12
	+		+	+	52.99	11.11
		+		+	53.03	11.15
			+	+	53.64	11.76
				+	55.92	14.04

			+		57.19	15.31

f) Presence of Harris´s Hawk

Elevation	Density of cows	%cov5-15	No. of stems	Canopy	AIC	ΔAIC
+	+	+		+	38.76	0
+	+	+			40.21	1.45
+	+		+	+	43.16	4.40
+	+		+		44.01	5.25
+	+			+	44.63	5.87
	+	+			47.31	8.55
+		+			48.58	9.82
+	+	+	+	+	48.94	10.18
+		+	+		49.67	10.91
	+	+	+		49.76	11.00
+		+		+	50.19	11.43
+	+	+	+		50.75	11.99

		+			51.37	12.61
	+	+	+	+	51.66	12.90
	+			+	51.97	13.21
	+	+		+	52.13	13.37
+					52.74	13.98
		+	+		52.86	14.10
+			+		53.07	14.31
+	+				53.25	14.49
		+		+	53.34	14.58
+			+	+	53.83	15.07
	+				54.15	15.39
+				+	54.16	15.40
		+	+	+	54.79	16.03
	+		+		55.04	16.28
	+		+	+	56.90	18.14
			+		57.11	18.35
				+	57.94	19.18

			+	+	59.03	20.27

g) Presence of Short-tailed Hawk

Elevation	Density of cows	%cov5-15	No. of stems	Canopy	AIC	ΔAIC
			+		43.60	0
+			+		44.93	1.33
	+		+		45.40	1.80
			+	+	45.54	1.94
	+				45.61	2.01
+					45.65	2.05
				+	46.13	2.53
+	+		+		46.93	3.33
+			+	+	46.93	3.33
+	+				47.42	3.82
	+		+	+	47.46	3.86
	+			+	47.59	3.99

+				+	47.60	4.00
+	+		+	+	49.24	5.64
+	+			+	49.41	5.81

h) Presence of King Vulture

Elevation	Density of cows	%cov5-15	No. of stems	Canopy	AIC	ΔAIC
	+	+	+	+	44.07	0
		+	+	+	47.90	3.83
			+	+	48.18	4.11
			+		48.69	4.62
+			+		49.34	5.24
	+		+		49.36	5.29
	+		+	+	49.49	5.42
+			+	+	49.74	5.67
+		+	+	+	49.86	5.79
			+	+	49.89	5.82

		+	+		49.89	5.82
+		+	+		50.02	5.95
+	+		+		51.24	7.17
	+	+	+		51.25	7.18
+			+		53.64	9.57
+		+			53.74	9,67
				+	53.74	9.67
+					54.25	10.18
	+				54.84	10.77
+				+	55.29	11.22
+	+				55.73	11.66
	+			+	55.74	11.67
		+		+	55.74	11.67
	+	+			56.50	12.43
+	+			+	57.14	13.07
+	+	+			57.16	13.09
+		+		+	57.24	13.17

	+	+	+	57.74	13.74
+	+	+	+	59.02	14.95

Chapter 7: Conservation priorities, management recommendations and the future of tropical raptor research

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7.1 Importance of raptor conservation

Raptor species are positioned at the top of their food web and, as such, are believed to play a relevant role in structuring biological communities (Terborgh et al. 2001; Sergio et al. 2006). It has been argued that removal of top predators affects other taxa, causing changes in abundance of species at lower trophic levels (Terborgh 1992; Silman et al. 2003). As top predators with large home ranges, raptors might be sensitive to habitat loss and fragmentation (Bierregard 1998; Thiollay 1998). Additionally, small population size increases the risk of local extinction for species (Purvis et al. 2000; Dale 2001; O'Grady et al. 2004).

There is an urgent need to document species population size of most raptor species and habitat attributes needed to maintain them, as well to develop new approaches for raptor studies that can provide robust information at low costs and in short times (Thiollay 1994; Bildstein et al. 1998). The most serious conservation threat for raptor species is habitat loss (Wilcox and Murphy 1985; Thiollay 1994, Bierregard 1998), whereas fragmentation of habitats poses a serious threat for species as they become isolated, affecting their viability and increasing extinction risk (Schaffer 1981; Kennedy 1986). It is important to rapidly measure species response to habitat change, particularly in the tropics

where most threatened raptor species occur and where habitat destruction is the fastest (Bildstein et al. 1998).

Habitat loss in Peru is an ongoing process so there is an urgent need to document the population size of species within the country and to devise effective methods to do this. Is also important to evaluate how species cope with changes in their habitats so effective conservation measures can be taken. With more than 70 species recorded, diversity of raptors in Peru is particularly high (GRIN 2012). This is also true for extreme northwest Peru, where 36 raptor species are found (Schulenberg et al. 2007; Piana, 2011). There is an urge to better understand the reasons that contribute to this unusually high diversity and maintain it.

7.2 The key findings of the PhD were:

In the study area, raptors were more diverse and abundant in the buffer areas followed by the reserve and the park, despite the last being under the highest level of protection. It is necessary to develop conservation schemes outside protected areas for the conservation of raptor species in northwest Peru. CCA identified certain floristic parameters that are relevant for raptor conservation in extreme northwest Peru, as they are key environmental features that may constrict the presence of species in the study area. Prevalence of larger trees such as Ceibo and the presence of a fuller vegetation stratum between 5 and 15 m might be particularly important for raptor species.

Habitat models generated for raptor species through Generalized Linear Models (GLM) showed the importance of vegetation structure parameters such as percentage of vegetation cover at different strata in influencing the distribution of species. Altitude, latitude and longitude were also relevant for at least six species because they determined climatic gradients that influenced forests composition and structure. For the Gray-backed Hawk, habitat models pointed at the importance of forested areas at moderate elevations east of the study site where Algarrobo, Polopolo, and Guasimo were absent, while for the Black Hawk-Eagle models highlighted the importance of forested areas at extreme altitudes (probably above 600 m asl) with full ground cover and with a high prevalence of Guasimo trees. For the King Vulture, a wide-ranging species that is uncommon in the study area, models pointed at the importance of forested areas with a fuller low vegetation stratum, and where tall trees, particularly Ceibo were absent.

Estimation of species densities through Distance sampling using linear transects provided absolute density estimations with a CV of less than 34% for eleven out of fifteen raptor species. Number of contacts required to estimate demographic parameters for these species were between 17 and 168, but for six species with 30 or less detections, %CV was close to 30%. Results obtained included the first population estimates for Gray-backed Hawk in Peru. Although inclusion of flying birds in density estimates could be interpreted as a violation of one of the Distances assumptions (the one stating that objects should be detected before evasive movements are performed), it was the only option possible to obtain

density estimates (and population size) of species that are very rarely encountered perched (eg. King Vulture, Short-tailed Hawk and Zone-tailed Hawk). However, individuals of these species should only be included in Distance Sampling when birds are flying in circles relatively close to the transect. Clustering of raptor species with similar detectability and density estimations for species with the use of multipliers also proved to be a good method to improve demographic parameters of rarer species. When the rare Bat Falcon was excluded from analysis, values of %CV of density estimates obtained with the use of multipliers were significantly lower than those obtained with CDS (t = 2.6, df = 11, P = 0.025).

Generalized Additive Models (GAM) for raptor species in the study area also showed the importance of vegetation structure (particularly vegetation cover from 5 to 15 m above ground) in influencing the distribution of five species and of those that were rare in the study area. Canopy height was important in explaining the distribution of three species. GAM showed different responses of species to cattle: While some species presence decreased with increased cattle density, others increased. However species that were threatened in the study area showed a negative response to increased cattle. GAM also identified cattle densities at which species reactions were disproportionally positive or negative, particularly for those that are of conservation concern or rare in the study area such as the Gray-backed Hawk, the Black Hawk-Eagle, the King Vulture and the Great Black Hawk. My findings also point at threshold levels of cattle densities that are either favourable or detrimental for these species in the study area.

These cattle threshold levels could be used by protected area managers for the maintenance of the whole raptor community and for the conservation single species in areas under different land uses within the NWBR.

7.3 Conservation priorities in the NWBR and in the Tumbesian Centre of Endemism

Among the target species, Gray-backed Hawk and Black Hawk-Eagle demand special attention from conservationists. Gray-backed Hawk is an endangered species that is endemic to the Tumbesian Zone and although it is able to use degraded and edge habitat, in Ecuador its population is declining due to land use changes (Vargas 1995; BirdLife International 2012). Given the increased insularity of forest fragments in western Ecuador, conservation of the species population in Peru might prove vital for its long term persistence. The Black Hawk-Eagle has a wide distribution within the neotropics, ranging from southern Mexico to northern Argentina and the central and west part of South America (BirdLife International 2012). Its population is decreasing due to habitat loss (BirdLife International 2012), and it may be facing a major threat west of the Andes in Peru and Ecuador, where it might be particularly sensitive to forest loss above 600 m asl.

In the last 60 years, habitat loss in the Tumbesian zone has been serious. It is estimated that in Tumbesian Ecuador, only 5% of the original forest cover remains (Dodson and Gentry 1992). In Tumbesian Peru, habitat loss and fragmentation caused by agriculture, cattle grazing and fuel wood extraction has

also contributed to forest loss and fragmentation (Ektvedt et al. 2012). Amount of habitat and fragmentation are key issues for the conservation of biological diversity (Fahrig 2003; Ribeiro et al. 2009). Fragmentation of forests and isolation of remaining forest patches in the Tumbesian Centre of Endemism might replicate that occurring in the Atlantic coastal forests of Brazil, probably one of the most endangered ecosystems in the world (da Fonseca 1985; Ribeiro et al. 2009). Machalilla National Park, the largest protected area in Tumbesian Ecuador, is approximately 250 km away from CANP (Best and Kessler 1995). Increased fragmentation might be the most serious challenge for species conservation in the Tumbesian zone nowadays, as it will further isolate wildlife populations from those occurring north and west of the continent, reducing their genetic viability and leading to local extinctions (Soulé and Simberloff 1986; Terborgh 1992). This is not only relevant for raptors, but for other endemic and threatened species like parrots and mammals that also occur in this area (SERNANP 2011).

Although current rates of habitat loss in Ecuador have decreased, in Tumbesian Peru is on the rise (Ektvedt et al. 2012; World Bank 2012). In the Tumbesian Centre of Endemism small, isolated forest patches remaining at lower altitudes west of the Andes that are surrounded by secondary forests contribute to maintain connectivity between larger forest patches, yet may be subject to further conversion as demand for productive soils increases (Becker and Agreda 2005). Although raptors may have greater dispersal abilities that other bird taxa, fragmentation can affect availability of prey and nesting sites (Thiollay 1996).

Protection of these forest patches might be vital to maintain connectivity between sub populations as they may act as stepping stones for individuals, fostering their dispersal and preventing inbreeding that leads to extinction (Schaffer 1981; Palomares et al. 2012). Management of matrix habitat surrounding forested patches through reforestation of critical areas (i.e. river margins) and the establishment of corridors including public and private lands can also enhance connectivity between isolated forest patches and prevent further extinction of species (Simberloff et al. 1992; Baum et al. 2004).

At a broader scale, habitat degradation and fragmentation in the Tumbesian Centre of Endemism should be targeted through an integrated approach implemented collaboratively at both sides of the border. National governments of Peru and Ecuador in collaboration with regional and local authorities should focus in designing a conservation strategy for Tumbesian forests as a whole. This should consider enhanced protection of existing protected areas that act as refugia for biodiversity and the preservation of forest patches between them.

7.4 Management recommendations for the NWBR

Within the NWBR, management efforts should attempt to increase proportion of habitats that are particularly threatened by human activities and where there is a high prevalence of vegetation parameters that influence the presence of raptor species that are rare or threatened in the study area. Habitat management interventions that promote additional amounts of vegetation cover or of individual tree species within the species realized niches, particularly on the

bottleneck axes of CCA, might have direct positive impacts on species conservation and in the maintenance of this highly diverse raptor community.

Cattle grazing as performed in Tumbes National Reserve depends on the periodical maintenance and rotation of pastures through controlled burning. Cattle ranchers tend to “accidentally” burn remaining forest so more grazing areas are created. Given that cattle also feeds on the understory of surrounding forest patches, moisture content close to ground level is reduced, increasing risk of burning. Destruction of forest for the creation of grazing areas has completely removed original forest in vast expanses in the TNR. This might be affecting connectivity with populations in southern Ecuador, particularly for small bird species like the Black-headed Spinetail (*Synallaxis tithys*), Henna-hooded Foliage-gleaner (*Hylocryptus erythrocephalus*) and other understory specialists (BirdLife International 2012). Abundance of threatened and endemic species like that of the Gray-cheeked Parrot (*Brotogeris pyrrhoptera*) has been reduced in fragmented areas inside the TNR where cattle is abundant (SERNANP 2011).

Management of the NWBR should prioritize effective control by reserve authorities during burning of cattle pastures to avoid further destruction of remaining forest stands. This should be accompanied by cattle exclusion from forest patches adjacent to pastures and from the CANP. The use of exclusion fences for cattle for the protection of gallery forests along water courses that may act as corridors for wildlife species will help maintain connectivity between the TNR and other portions of the NWBR.

Initiatives to substitute dependence of local population on extractive activities conducted inside the reserve should prioritize the training of local people to provide services for tourists, as has been done in the lowlands of Peru and Bolivia (Stronza and Gordillo 2008; Jamal and Stronza 2009). Given the elevated number of endemic bird species in the NWBR and the relatively easy access from the city of Tumbes, bird watching tourism could be promoted. Training local young people on bird identification could foster their involvement in tourism activities and habitat conservation. However, it is vital that the road that connects the town of Pampas de Hospital with El Caucho Research Station is periodically maintained, especially after the end of the rains.

7.5 The future for raptor surveys in the NWBR

In Tumbesian Peru and Ecuador dispersion rate and recruitment of raptor species in degraded forests should be evaluated. This should prioritize monitoring of Gray-backed Hawks and the Black Hawk-Eagles that might be moving from the NWBR towards northwest Ecuador. Additionally it is urgent to evaluate breeding, survivorship, recruitment and habitat selection of Gray-backed Hawks established in the north eastern part of the TNR; particularly those individuals located north and west of Cerro Linda Chara, since these areas have been greatly degraded due to cattle ranching. Monitoring populations of recently reported Solitary Eagles in PNCA (Piana 2011) should also be prioritized.

7.6 Future research directions in tropical raptor ecology

Habitat fragmentation is an ongoing process in forested tropical areas of the world (FAO 2001; Benhin 2006). It is expected that more species will go under threat as their main habitats are reduced in extension (Sayer and Whitmore 1991; Brooks et al. 1997). This might be particularly relevant for large raptor species with large territorial requirements and long reproductive periods such as eagles and vultures (Accipitridae and Cathartidae) (Terborgh 1974; Thiollay 2006). It is important to estimate population sizes of forest-dependant tropical eagles, particularly those inhabiting islands that are ongoing rapid fragmentation in southeast Asia and those occurring along the Andean slopes of Colombia, Ecuador and Peru (Collar 1986; Thiollay 1996; Gjershaug 2006). Habitat modelling for these species can provide information on the most relevant habitat parameters that influence their presence and thus can help in allocating scarce resources (both technical and monetary) more efficiently for their preservation.

Distance sampling proved to be a useful and easy to implement survey method to estimate demographic parameters of raptors in the study area. Compared to frequently used raptor abundance index along roads, Distance sampling additionally demands measuring the perpendicular distance from individuals to transect and this can be easily achieved with a range finder. Given the urgent demand to estimate demography parameters of tropical raptors (Bierregard 1998; Bildstein et al. 1998), Distance sampling should be encouraged among researchers aiming to estimated absolute density and population size of tropical raptors.

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