ECOLOGY AND CONSERVATION OF LARGE-BODIED AVIAN FRUGIVORES OF LUZON, PHILIPPINES

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ABSTRACT

Avian frugivores across Southeast Asia, and in the Philippines in particular, are seriously threatened owing to massive loss of habitat and direct exploitation through hunting and the pet trade. Their declines may have dire consequences for wider ecological processes as many frugivores are also seed dispersers. Conservation programmes in the Philippines are crippled by a lack of knowledge on the status, abundance and ecology of frugivores which extend to other endemic species in the country. This PhD identified factors that influenced frugivore community composition as well as drivers of frugivore distribution across Luzon, the largest island in the Philippines. It also developed cost-effective methods for gathering baseline ecological data to inform conservation measures for frugivores and other little-known species over large geographical areas. This included a way of correcting for the bias caused by non-random transect placement in a study site which is often the case during bird surveys in the tropics.

Twenty-five species of pigeons, parrots and hornbills were surveyed using distance sampling along nearly 500 km of line transects at 14 sites across the island of Luzon. I documented surprisingly few reliable disappearances of frugivores from individual forest patches – in fact this and other fieldwork since 2000 has increased the known extent of occurrence of several species. However, green racquet-tail *Prioniturus luconensis* may have suffered a real range contraction. More alarming was the absence of large parrots from most sites with apparently intact habitat surveyed. Even where present, large parrots exhibited lower densities than related species in similar habitat in Southeast Asia. For six species, including four of six parrots, the largest estimates of population in any reserve in Luzon numbered < 1000 individuals, and nearly one-third of all populations in reserves were < 100. At minimum viable population (MVPs) of 500, frugivore communities in all but 2–3 of the largest reserves are not expected to remain intact. Although seed dispersers may fare better than seed predators (large parrots), a major collapse of frugivore communities may occur across Luzon, with serious implications for ecosystem functioning.

The Philippines comprise islands of different origins, climate and habitat, a situation which is expected to produce a biogeographically complex set of animal and plant communities, which themselves are influenced by anthropogenic actions. I explored similarities between frugivore communities across 24 sites in Luzon using non-metric multidimensional scaling and attempted to explain site differences in terms of a series of geographical, habitat, and disturbance predictors using Mantel tests. In both analyses using species presence/absence and densities, sites/species did not seem to ordinate simply according to region. Consistent outliers included three sites in West Luzon and two in Central Luzon, and, in terms of species, several large rare parrots and pigeons. The strongest correlates of site dissimilarity were differences in altitude and several human disturbance measures, including path width, canopy closure and a 'human impact index' (reflecting human pressures and forest management). While Luzon's frugivore communities have been no doubt shaped by natural biogeographical processes, their effects have been largely obscured by anthropogenic environmental degradation. There is an urgent need to understand better the drivers of frugivore species distribution in order to develop appropriate conservation management strategies. To identify precise habitat associations of 18 avian frugivores, the presence/absence of each species along 400 m long segments of 213 transects was examined in relation to vegetation structure and composition, measured at 1227 plots, using generalised linear mixed models (the 24 sites were entered as a random factor). Individual frugivore species showed unique patterns of association with habitat variables but five species were high-altitude specialists while six preferred lowland sites. Another six species strongly preferred primary forest while one thrives in disturbed forest with the attendant increase in food availability. I then ran generalised additive mixed models (GAMMs) to identify any non-linearities in responses of species to habitat features. Relationships with habitat variables were on the whole simple linear or quadratic for the majority of species, suggesting that there were gains to be had in improving habitat right along the disturbance gradient.

Precise and accurate estimates of wildlife population density and sizes are essential to evidence effective conservation programmes. Line transect distance sampling is a robust method in that variability in detectability due to distance from the transect line, but many conservation studies cannot, by necessity, be based on random transect placement, but instead use transects along existing trails. This study estimates the bias in abundance estimates due to non-random placement of transects along hunter trails (path width <100cm) and access roads (path width >100cm) as compared with random paths (especially cut transects). Path types were similar in altitude, but differed in terms of tree girths, slope, canopy covers, and presence of crops. Hunter trails yielded lowest densities and encounter rates for nine of 12 species and lowest effective strip width for seven of 12 species. Highest densities and encounter rates were along random paths for seven of 12 species. Differences in density across trail types were driven by differences in encounter rates rather than differences in detectability. Density estimates calculated from surveys which used non-random transects should be upwardly corrected by on average 90% (18-187%). In fragmented forests where random placement of transects is not always possible, this method of correction will allow species density estimates from sampling along hunter trails and access roads to be adjusted.

Top on the list of research and conservation priorities arising from this PhD would be to map the remaining populations of the Luzon-endemic Green Racquet-tail, Luzon Racquet-tail and Flame-breasted Fruit-dove and to formulate conservation intervention measures for these threatened/near-threatened species taking into account habitat preferences and threats to the species. Forest and reserve management programmes and policies in the Philippines and elsewhere in the tropics would greatly benefit from empirical data on species occurrence and accurate estimates of population abundance using methods described in the study. Sound ecological research by local biologists/ecologists must be encouraged to further our understanding of species requirements, species tolerance to disturbance, and viability of populations, especially of the many unique and/or threatened species in the Philippines and the wider SE Asia region.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

Number *Page*

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Chapter 1

ECOLOGY AND CONSERVATION OF PARROTS AND OTHER LARGE AVIAN FRUGIVORES OF LUZON, PHILIPPINES

1.1 Ecology and conservation of parrots and other large avian frugivores: the Philippines in context

Nearly half of the Philippines' terrestrial vertebrate fauna is endemic and about a quarter of this is threatened, securing the country "the hottest of hotspots" designation among 34 biodiversity hotspots in the world (Myers *et al.*, 2000, Conservation International, 2007). A very high proportion of threatened birds found in the country are endemic: 81% (60 endemic out of 74 threatened species) (BirdLife International, 2013). Forest loss due to logging, mining and slash-and-burn farming as well as direct exploitation for food and the pet trade have been identified as the major threats to the Philippines' endemic birds (BirdLife International, 2003). Of twelve Philippine parrot species, all but one is endemic, and eight are globally threatened with extinction (IUCN, 2011). Likewise, six out of nine hornbills in the country, all endemic, are threatened, the highest number for any country (IUCN, 2011). Pigeons are not spared, with 13 out of 34 species in the threatened (4 Vulnerable, 2 Endangered and 4 Critically Endangered) and near-threatened categories (IUCN, 2011).

The situation is compounded by a chronic lack of information on endemic species, this extending even to charismatic forms such as parrots (Collar 1998) and large frugivores. As a case in point, the nest and breeding behaviour of the common and endemic parrot Guaiabero *Bolbopsittacus lunulatus* has only been recently described by birdwatchers and photographers (Rosell II *et al.*, 2007, Arndt, 2005). A cursory scan of the definitive guide to Philippine birds yielded five endemic parrots and 11 endemic/near-endemic pigeons without breeding information (Kennedy, 2000).

Seed dispersal by frugivores is probably one of the most important among the many vital ecological and social services that birds provide (Whelan *et al.*, 2008, Sekercioglu, 2006). Consequently, changes in frugivore assemblage, declines in their population or possible future extinction threaten further the already dwindling tropical forests in the Philippines and the communities they sustain. Moreover, the biological diversity in the Philippines is not yet fully established with at least 270 plants, terrestrial birds, mammals, reptiles and amphibians discovered in the past 25 years, not including insects, marine life, and new species awaiting description (de Leon and Lita, 2012). Conservation action is desperately needed as the likelihood is high of many species becoming extinct before they are discovered. The present study was designed in part to narrow the information gap on frugivore ecology in order to direct future conservation action.

1.2 Environmental change in the Philippines

1.2.1 The importance of the Philippines as a hotspot

A combination of exceptional levels of endemism and serious levels of habitat loss characterize biodiversity hotspots, a concept adopted by Conservation International in 1989 as its institutional blueprint (Myers *et al.*, 2000, Conservation International, 2007). It sought to prioritize conservation action around the world in areas of highest threat to habitat and high levels of species endemism by setting a requirement of at least 1,500 species of endemic vascular plants and at least 70% loss in original habitat for a region to qualify as a hotspot (Conservation International, 2007). This conservation prioritization scheme was followed by Mittermeier *et al.* (1997), who identified 17 "megadiversity" countries throughout the world that collectively harbour more than two thirds of the world's biological wealth (Mittermeier *et al.*, 1997). The Philippines is both a megadiversity country and biodiversity hotspot in its entirety (Myers *et al.*, 2000, Conservation International, 2007). It is considered by many as the world's biologically richest country, having the highest number of unique terrestrial and freshwater species (and threatened unique species accordingly) per unit area, with most of the species crammed in only 7% remaining original vegetation (See Table 1.1) (Conservation International, 2007, Heaney and Regalado, 1998). Birdlife International has identified 117 Important Bird Areas (IBA) and 10 Endemic Bird Areas (EBA) in the country (BirdLife International, 2003, Chan *et al.*, 2004, Mallari *et al.*, 2001). In terms of marine biodiversity, the country is recognized as the "epicentre of biodiversity and evolution" and apex of the "Coral Triangle", the region of highest concentration of marine species whose other angles are Sumatra and the Solomons (Allen and Werner, 2002, Carpenter and Springer, 2005). For this reason, the Philippines' biological diversity has been referred to as comparable to the Galapagos Islands multiplied tenfold (Heaney and Regalado, 1998).

Table 1.1 Percent endemism in major taxonomic groups in the Philippines.

Taxonomic Group	Species	Endemic Species	Percent Endemism
Plants	9,253	6,091	65.8%
Mammals	194	122	62.9%
Birds	632	206	32.6%
Reptiles	350	245	70%
Amphibians	110	88	80%
Freshwater Fishes	343	83	24.2%
Butterflies	910	360	39.6%
Total	11,792	7,195	61%

1.2.2 Regional biogeography, ecology and conservation

The world's second largest archipelago after Indonesia, the Philippines encompasses more than 7,100 islands with a long and complex geological history dating back some 30-50 million years ago (Heaney, 1986, Hall, 2002, Heaney *et al.*, 2005). Most of the islands in the archipelago started as "island arcs" of volcanic or geologic origin on the Philippine Sea Plate at the edge of the Pacific, and were transported through plate tectonic and volcanic processes to their present location (Hall, 2002, Heaney and Regalado, 1998). Around 50 million years ago, movement of the Australian continent northward resulted in uplift, subduction, and convergence of these island segments where it collided with the continental plate of Asia (Heaney and Regalado, 1998). Small but permanent islands formed from this uplift around 30 million years ago but it was not until 15 million years ago that a large island was formed which constituted parts of the present northern Luzon, while much smaller islands made up the southern Philippines (Heaney and Regalado, 1998). Before the Miocene, Luzon was connected to northern Borneo and Sabah through the Sulu-Cagayan Arc (Hall, 2002). When the Halmahera-East Philippines-South Caroline Arc collided with New Guinea, it caused the Philippine Sea Plate to rotate, resulting in the convergence of the north and south Philippines from around 25 million years ago (Hall, 2002). Around the same time during the Neogene, Luzon started to separate from the proto-Sulu-Cagayan Arc (Hall, 2002). It was not until the Late Miocene that the Philippine archipelago formed a single region at the margin of the Philippine Sea Plate (Hall, 2002, Heaney and Regalado, 1998). Mindoro, Busuanga, parts of Panay, and northern Palawan are the only islands of continental origin in the archipelago which are thought to have originated as crusts rifted from the South China margin and approached the northern Philippine Islands by the end of the Miocene (Hall, 2002, Mey, 2003).

Recent geological history, however, is responsible for the present configuration of the Philippine archipelago. It was during the most recent period of low sea level in the Pleistocene that the current islands coalesced into four large islands: Greater Luzon, Greater Mindanao, Greater Negros-Panay, and Greater Palawan. These "Pleistocene islands" arose as new oceanic islands from the ocean floor having no dry-land connection with mainland Asia (except for Palawan) or other islands and continents (Heaney *et al.*, 2005). It is this long and complicated geological history together with the tropical location, diverse climate and uneven topography in the Philippines that are mainly responsible for their remarkably high degree of endemism (Conservation International, 2007, BirdLife International, 2003).

1.2.3 Environmental problems in Philippines

The ratio of threatened endemic plants and vertebrates per unit area in the Philippines is highest among all biodiversity hotspots (Myers *et al.*, 2000). Many causal factors have been identified which account for this widespread threat to biodiversity. These have varying degrees of severity at sites and appear to act in concert, so that oftentimes the impact from each cannot be reasonably separated.

- *Loss and degradation of forests*

The country has lost around 93% of its original forest cover in the last 500 years, of which 55% were lost only after World War II (Kummer and Turner II, 1994, Kummer, 1992). Logging was by and large a sustainable enterprise during the pre-colonial period. Forest cover was at 90% of the land area at the start of the Spanish occupation in 1521 (Westoby, 1989). Forest clearing and timber extraction during the more than 300-year Spanish occupation allowed the expansion of commercial crops, e.g. sugarcane, abaca and tobacco that supplied international markets, whilst also providing building materials for the burgeoning galleon trade (Garrity *et al.*, 1993). Unlike customary Filipino systems of land tenure, the Spanish instituted state ownership and centralized management of forest land and resources (Pulhin, 2002). Logging as a large-scale commercial enterprise, on the other hand, was introduced by the American colonizers. From 70% at the start of the American occupation in the 1900s, old growth forest was reduced to 30% by the time the Americans left in the mid-1940s. Harvesting of logs was unrestricted and mainly for export abroad to sustain the industrialization of North America (Ghee and Valencia, 1990). But the most blatant period of drastic loss to the country's forest resources was during the presidency of Ferdinand Marcos (1965-1986), who awarded Timber Licensing Agreements (TLAs) to loyalists and supporters. At the height of logging activities in the 1970s TLAs, which were valid for 25 years and renewable for another 25 years, covered one-third of the land area of the country and were possessed by only 97 companies or families of the political elite (Lasco *et al.*, 2001). Deforestation rates peaked at 300,000 hectares annually and resulted in the loss of seven million hectares of forest during the Marcos regime (Chokkalingam *et al.*, 2006, Kummer, 1992). The Philippine logging industry made $42.85 billion profits (or $2.65 billion yearly) during the period 1972-1988 (Teehankee, 1993).

A predominant pattern of deforestation is evident in the Philippines where old growth forests are converted to secondary forest through logging with subsequent removal through illegal logging, and shifting and permanent agriculture (van der Ploeg *et al.*, 2011, Teehankee, 1993). More than half of the Important Bird Areas (IBA) are affected by slash-and-burn farming or *kaingin* which is a form of shifting agriculture (BirdLife International, 2003). *Kaingin* is mostly practised by poor, landless peasants in the uplands (BirdLife International, 2003). It is estimated that half of the 48 million rural population (The World Bank, 2011, Pulhin, 2002) or a third of Filipinos in the country (Liu *et al.*, 1993) live in the upland and are largely dependent on forest resources that remain in these areas. Another destructive agricultural practice is the periodic burning of secondary forest for cattle pasture maintenance. Both practices put a halt to forest regeneration and significantly contribute to soil erosion, as many of these areas have slopes of ≥ 18 percent (Myers, 1988, Chokkalingam *et al.*, 2006). Without land tenure instruments in place, this trend of land clearing for agriculture is expected to increase as the human population increases by 1.2% in rural areas each year (The World Bank, 2011).

Forestry practices that put a premium on timber extraction was the norm for many decades. A career in forestry used to mean prosperity for many rural families. Forestry schools in the past mainly catered to the needs of the timber industry with training for foresters focused on methods of timber extraction and processing. But with the changing political atmosphere after the fall of the Marcos dictatorship in 1986 and the passage of key forestry legislation, the balance turned from pro-elite and exploitative methods towards pro-people and participatory policies in forest management (Pulhin, 2002). One such law was Republic Act (RA) 7160 or the Local Government Code in 1991 which devolved certain DENR responsibilities to local government units (LGUs) and empowered the LGUs to create and enforce forestry laws and promote community-based forest management (CBFM) among their constituents. This was followed by RA 7586 or the National Integrated Protected Area System (NIPAS) Act of 1992, which provided for the representation of indigenous peoples and local stakeholders on the Protected Area Management Board—the administering body that decides on policies and matters pertaining to protected areas. Another landmark policy was Executive Order No. 263 which adopted CBFM as the national strategy for sustainable forestry. Finally, 1997 saw the passing of an important law which has been considered as the "watershed proclamation in the history of the Philippines' forest legislation" (Pulhin, 2002)—RA 8371 or the Indigenous Peoples Rights Act of 1997, which recognized the right of indigenous communities over ancestral lands which until then was under state control.

- *Mining*

Mining poses a major threat to the Philippine environment. The Philippines is rich in mineral deposits which include gold, copper, nickel, chromite, manganese, silver and iron

(Mines and Geosciences Bureau, 2012). According to the Mines and Geosciences Bureau (MGB) (2012) the Philippines was ranked first in the world with the largest iron ore, third in gold, fourth in copper, fifth in nickel and sixth in chromite deposits. The US State Department on its updated country fact sheet released in early 2012 estimated Philippine mineral deposits to be $840 billion worth (P36.64 trillion at P43.62 per US dollar) (Agence France-Presse, 2012). Profits from gold mining alone can potentially contribute $16.87 billion (P7.36 trillion) or 76% of the country's GDP of P9.73 trillion in 2011, an amount supposedly enough to eradicate poverty in the country. However, the way the industry is run, which disproportionately benefits mining companies and the central government over local government units and communities being devastated by mining, has caused poverty rates to increase in areas with large-scale mining. The direct reason for this increase in poverty is that communities based on traditional livelihoods such as farming and fishing are being displaced as mountains and land are destroyed by mining operations. The poor performance of the industry in the past decade has cast doubts on its long-term economic benefits when weighted against its well-documented and oftentimes long-term damage to the environment, particularly to biodiversity, water systems, and land viability.

- *Development*

While road systems undoubtedly aid economic development in far-flung rural areas by facilitating the transfer of farm goods to the market, it could also lead to increased forest loss and devastation through illegal logging and settlement by *kaingin* farmers along roads. In fact, Liu *et al.* (1993), in a study analysing the rates and patterns of deforestation in the Philippines from 1934 to 1988, found higher rates of deforestation nearer roads. This is especially critical in sensitive habitats and reserves supporting threatened species and indigenous communities. Logging and mining can also result in siltation that can harm riverine habitats as well as pollution from mine tailing that could potentially bioaccumulate in top predators, affecting their reproductive output. Fifteen years after the mine spill disaster that killed the pristine waters of the Boac river in Marinduque, toxic mine tailings still threaten the livelihoods and lives of communities living in the area (Silverio, 2011). Similarly, the trend of increasing reliance by farmers on inorganic fertilizers, herbicides and pesticides must be controlled to minimize pollution in rivers.

- *Direct exploitation*

Forty percent of birds in the Philippines are hunted for food and/or sport, with pigeons and hornbills especially vulnerable due to their habit of flocking on fruiting trees (BirdLife International, 2003). The Wildlife Resources Conservation and Protection Act (RA 9147) prohibits hunting of all wildlife in the Philippines apart from members of indigenous communities, who are allowed small-scale hunting using traditional methods. Upland communities in the Cordillera in north-west Luzon traditionally practise nocturnal hunting using a strong light source and nets set along paths of bird migration along mountain tops. However, monitoring and enforcement are so weak that hunting remains unabated in many parts of the country and even inside reserves. Fruit-eating birds, bats, civets and wild pigs are prized by poachers among 22 invertebrate and vertebrate species hunted in a national park in southern Luzon, Philippines (Scheffers *et al.*, 2012). Another critical and direct threat to biodiversity is commercial wildlife trade, which affects 20% of threatened birds in the Philippines including several pigeons, parrots and hornbills as well as the colourful Palawan Peacock-pheasant *Polyplectron napoleonis* (BirdLife International, 2003). The endemic Philippine Cockatoo *Cacatua haematuropygia*, which occurred on just eight islands in the period 1989-1994 from 52 islands originally, has seen the most drastic drop in population and distribution, mainly due to trapping for the pet trade (BirdLife International, 2001). Survival of trapped nestlings and birds is 50% for the Philippine Cockatoo and 20% for the Palawan Peacock-pheasant (BirdLife International, 2003). The Green Racquet-tail *Prioniturus luconensis*, which used to occur in big flocks near population centres in the Sierra Madre (Poulsen, 1995), was encountered just twice during our 2010 survey (Española *et al.*, 2013).

1.2.4 Protected area provision in the Philippines

Eleven percent of the Philippines' land area is under protection, although only 6% falls under the IUCN categories I-IV (IUCN and UNEP-WCMC, 2010). This falls below the international minimum target of 10% of the total land area. Protected area distribution is also skewed towards protection of higher elevation areas which are biologically unrepresentative, since the highest levels of biodiversity are found in low elevation forests (Mackinnon, 2002, Mallari *et al.*, 2011). Protected area coverage of biogeographic regions and centres of species endemism (e.g. endemic bird areas) is likewise uneven with a bias towards Palawan, Mindoro and oceanic islets, and poor coverage of the biologically rich and larger islands of Luzon and Mindanao (Mackinnon, 2002). Moreover, boundaries of forest and protected areas do not always overlap, so that degraded and converted habitats are often included in protected area boundaries while remaining natural lands are not protected (Mackinnon, 2002). Of the 224 protected areas under the NIPAS, only 132 (<60%) overlap with priority conservation areas identified during the second iteration of the national biodiversity strategy and action planning workshop in 2002 (Ong *et al.*, 2002). These 206 priority sites identified together with the 425 threatened Philippine species (IUCN, 2011) form the framework within which conservation research and programmes need to be conducted in the country (Ong *et al.*, 2002).

Management of reserves and sanctuaries has been fraught with problems since NIPAS was enacted, mainly due to lack of resources. The PAWB does not have the resources to provide sufficiently for the infrastructure, manpower and site management capability necessary for effective protection of reserves (BirdLife International, 2003). The lack of manpower to patrol forest reserves, combined with corruption in the forestry service and municipal governments, has resulted in protected areas becoming susceptible to exploitation from illegal logging and hunting (van der Ploeg *et al.*, 2011, Scheffers *et al.*, 2012).

1.3 Frugivore ecology

1.3.1 Frugivore species diversity and taxonomy

Frugivore (fruit-eating) species are the main seed dispersers of plants with fleshy fruits. Species richness and composition of frugivores vary across the major biogeographical realms (Afrotropics, Australasia, Indo-Malaya, Nearctic, Neotropics and Palearctic). Corlett (1998) made a review of frugivore diversity in the Oriental (Indomalayan) region, which has one of the most abundant and diverse frugivore assemblages worldwide with half the genera of terrestrial mammals and more than 40% of bird genera as well as many fish and reptile species having some degree of frugivory in their diet (Table 1.2). Species highly dependent on fruit for their diet occurred in two families of reptiles, 12 families of mammals and 17 families of birds (Corlett, 1998). It must be noted that families Bucerotidae (hornbills) and Columbidae (pigeons) are of major importance in their role as seed dispersal agents because most of the species in these families are obligate frugivores and most of the seeds in the fruits they consume survive gut passage. Conversely, it is not known whether members of family Psittacidae (parrots) in the Orient are entirely seed predators as some parrots are known to disperse a percentage of the seeds they consume (Young *et al.*, 2012).

Table 1.2 Frugivory and seed dispersal by Oriental vertebrates. Doubtfully and biogeographically marginal taxa are excluded. Frugivory: 1, occasional; 2, consistent; 3, fruit seasonally dominant; 4, majority of annual diet. Seed survival refers to proportion of seeds which survive oral processing and, if swallowed, gut passage. Importance is the predicted impact of local extinction of the taxon on plant communities through loss of seed dispersal services: 1-4, minor to major. Table adapted from Corlett (1998). * are taxa that occur in the Philippines. 🕊are taxa covered by the current study.

Taxon	**Frugivory**	**Seed survival**	**Importance**
Fish			
Cyprinidae*	0±3	?	?
Pangasiidae*	0±3	?	
Clariidae*	0±3	?	?
Reptiles			
Emydidae	0±3	Most?	?
Testudinidae*	0±3	Most?	?
Agamidae*	0±2?	Most?	?
Scincidae*	0±2	Most?	?
Varanidae*	0±3	Most	1
Mammals			
Phalangeridae	1±2	Most?	?
Erinaceidae	0±2	?	?
Tupaiiadae*	3	Most	1
Pteropodidae*	4	Most	4
Loridae*	1	Most	1
Cercopithecidae*			
Cercopithecinae*	3±4	Most	3
Colobinae	1±2	Few	0
Hylobatidae	4	Most	4
Hominidae	4	Most	3
Canidae	1±3	Most	2
Ursidae	3±4	Most	2
Ailuridae	2	Most	1
Mustelidae*	1±3	Most	1
Viverridae*	0±4	Most	4
Herpestidae	1±2	Most	1
Felidae*	0±1	Most	0
Elephantidae	2	Most	2
Tapiridae	2	Most	2
Rhinocerotidae	2	Most	2
Suidae*	2	Some	1
Tragulidae*	4	Some?	2?
Cervidae*	2	Some	2?
Bovidae*	1±3	Some	2
Sciuridae*	0±4	Few	?
Muridae*	0±4	Some	1
Hystricidae*	2	Few?	?
Leporidae	1±2	Few?	?
Birds			
Megapodiidae*	2	?	?

Table 1.2 continued

Taxon	**Frugivory**	**Seed survival**	**Importance**
Phasianidae*	2±3	Some	2
Picidae*	1	?	?
Megalaimidae*	4	Most	4
Bucerotidae*🕊	4	Most	4
Trogonidae*	1	?	?
Cuculidae*	1±3	Most	2
Centropididae*	1	?	?
Psittacidae*🕊	4	None?	0
Columbidae*🕊			
Ducula, *Ptilinopus*, *Gymnophaps*	4	Most	4
Other genera	1±4	Few	1
Otididae	1±3	Most?	1
Rallidae*	1	?	?
Pittidae*	1	?	?
Eurylaimidae*			
Calyptomena	4	Most	3
Other genera	1	?	?
Meliphagidae	2	Most	1
Irenidae*	2±3	Most	2
Corvidae*	1±3	Most	2
Muscicapidae*			
Turdinae*	2±3	Most	2
Muscicapinae*	1	Most	1
Saxicolini*	1±3	Most	2
Sturnidae*	2±4	Most	3
Paridae*	1±2	Few	?
Pycnonotidae*	3	Most	4
Zosteropidae*	3	Most	3
Sylviidae*			
Acrocephalinae*	1	Most	0
Garrulacinae	1±3	Most	2
Timaliini*	1±3	Most	3?
Nectariniidae*			
Dicaeini*	2±4	Most	2
Nectariniini*	1	Most	0
Passeridae*	0±2	None?	0
Fringillidae*	0±4	Few?	0

The global distribution of frugivory in birds points to the Neotropics as the most species-rich biogeographical realm in terms of both overall bird diversity and frugivore richness (Kissling *et al.*, 2009). The other realms and regions along equatorial latitudes—Indonesia and New Guinea, but not Africa—also show high proportions of frugivores in bird assemblages (Kissling *et al.*, 2009). Low diversity of frugivorous bird species in the

Afrotropics was reflected in the very low species richness of fleshy-fruited plants (Snow, 1981, Kissling *et al.*, 2007). In Southeast Asia, the dominance of non-fleshy fruited trees (Dipterocarpaceae) west of Wallace's Line may have given rise to the lower frugivore richness in the realm compared to the Neotropics (Primack and Corlett, 2005). It must be mentioned that primate diversity west of Wallace's Line may have a role in inhibiting avian frugivory diversification as parrot and pigeon richness greatly increase in Indonesia in the absence of primates except for Sulawesi. Kinnaird and O'Brien (2005) did find less complex hornbill and primate assemblages in Sulawesi, which is within Wallacea, compared to Sumatra within the Asian biogeographic realm, although biomass for both groups was significantly higher in Sulawesi. The higher numbers of frugivorous species in the Indo-Malaya/Oriental region and New Guinea compared to the Afrotropics may be explained by the high diversity of a keystone resource (fig trees, *Ficus* spp.) in the Indo-Pacific region (Lambert and Marshall, 1991, Kissling *et al.*, 2007, Kissling *et al.*, 2009). Fruit fall was found to be 1.7 times larger in tropical forests than in temperate forests, which to a degree explains higher frugivore diversity in the tropics (Hanya and Aiba, 2010).

Among frugivorous birds worldwide, the most numerous (50%) are in the order of perching birds (Passeriformes) followed by the woodpeckers and allies, which include toucans and barbets (Piciformes), parrots (Psittaciformes) and pigeons (Columbiformes), which made up 9%, 11% and 15% of all frugivores respectively (Kissling *et al.*, 2009). The remaining 11 orders made up less than 4% of all frugivores. Orders with exclusively frugivorous species include the African turacos (Musophagiformes) and African mousebirds (Coliiformes), while pigeons (Columbiformes), chachalacas, guans and curassows (Craciformes) and the hornbills (Bucerotiformes) had more than 50% frugivorous species. Other orders had <10% frugivorous species: Galliformes, Cuculiformes, Gruiformes and Strigiformes. The Passeriformes, Piciformes and Craciformes have highest frugivore richness in South America, Psittaciformes in the Amazon basin, Bucerotiformes in Indonesia, and Columbiformes in New Guinea (Kissling *et al.*, 2009).

Frugivore species composition on islands is different from mainland species, with lizards that feed on nectar, pollen and fruit being one of the main agents of pollination and seed dispersal (Olesen and Valido, 2003). The Philippine islands have three such remarkable lizards, with two having been discovered recently—the only monitor lizards (*Varanus* spp) known to be mainly arboreal and frugivorous (Sy *et al.*, 2009, Gaulke *et al.*, 2009, Gaulke, 2010, Welton *et al.*, 2010). Another important reptile seed disperser on islands is the tortoise, which was observed feeding on > 45 plant species in the Galapagos (Blake *et al.*, 2012). These tortoises were found to have very long mean gut retention times of 12 days (28 days maximum) with an average seed dispersal distance of 394 m (4,355 m maximum). Their faeces have also been found to contain, on average, 464 seeds of 2.8 species per dung pile. Finally, an unusual insular seed disperser is found in New Zealand—a giant, flightless orthopteran that consume fleshy fruits and disperse seeds after gut passage (Larsen and Burns, 2012).

1.3.2 Seed dispersal and ecosystem functioning

Frugivore abundance and richness has been found to positively affect the probability of seed dispersal into deforested areas, which indicates that in order to preserve a complete seed dispersal service the whole assemblage of frugivores must be conserved (Garcia and Martinez, 2012). Loss of disperser species often results in dispersal failure for a plant species (Babweteera *et al.*, 2007, da Silva and Tabarelli, 2000, Terborgh and Nuñez-Iturri, 2006). Coupled with recruitment failure beneath parent plants, dispersal failure can lead to extinction of plant populations (Temple, 1977) or at the very least reduce plant reproductive success, resulting in population decline over time (Levin *et al.*, 2003, Wotton and Kelly, 2011). Higher germination rates have been shown in dispersed rather than undispersed seeds, with higher growth and survival of juvenile plants growing away from the parent plants (Bleher and Bohning-Gaese, 2001, Asquith *et al.*, 1999). Dispersal failure inhibits recolonization of forest fragments or clearings after local extinction, resulting in increasingly clumped distribution of plants and consequently increased susceptibility to stochastic disturbances (Fahrig and Merriam, 1994). Moreover dispersal failure has implications for the survival of plant populations under pressure from climate change due to their inability to migrate over long distances (Corlett and LaFrankie, 1998, Primack and Miao, 1992).

Nevertheless, the majority of rainforest plants rely on multiple species for seed dispersal, so it is unlikely that plants will have lost all of their dispersal potential from a complete absence of primary disperser species (Cordeiro and Howe, 2003). Reduced numbers of frugivores have been empirically shown to lower rates of visitation and fruit removal (Cordeiro and Howe, 2003, Bleher and Bohning-Gaese, 2001, Pizo, 1997). In Ecuador the hunting of frugivores such as toucans and primates, which are responsible for nearly 85% of visits to a fruiting tree, with toucans recorded in 74% of visits, directly impacts fruit removal rates: fruiting trees at non-hunted sites had more seeds removed (89.4%) than at hunted sites (66.8%) (Holbrook and Loiselle, 2009).

Frugivore species richness was determined by species richness of *Ficus* in sub-Saharan Africa, more so than water-energy and habitat heterogeneity variables (Kissling *et al.*, 2007). However, in another study comparing global patterns of avian frugivory, water-energy dynamics and productivity were the best predictors of vascular plant and therefore bird diversity via climatic effects on food plants specifically on fruit production and fruiting phenologies (Kissling *et al.*, 2009).

Variation among frugivores is primarily a function of the plant species they consume and disperse (Snow, 1981, Innis, 1989, Crome, 1978). This variation in turn is affected by the morphological, physiological and behavioural traits of frugivore species and the morphological, chemical and nutritive traits of fruits (Corlett, 1996, Poulsen *et al.*, 2002, Kitamura *et al.*, 2002, Kitamura, 2011, Levey *et al.*, 2002, Wilson and Downs, 2012). The manner of plant consumption between mammals and birds differ due to their physical makeup, with mammals consuming large and/or hard fruits with their teeth while birds are limited in their ability to consume large fruits by the size of their beaks and gape widths (Moran *et al.*, 2004, Moran and Catterall, 2010). Patterns of fruit consumption in 'bird', 'bat' and 'terrestrial mammal' dispersal syndromes are described in terms of fruit characteristics including size, colour, pulp characteristics and location on a plant, and frugivore characteristics including perception of fruit colour or odour, digestive function, and feeding or foraging behaviour (Moran and Catterall, 2010, Moran *et al.*, 2004).

Fruit size is a major characteristic considered in the choice of fruit by disperser species, and this in turn is constrained by frugivore body weight and gape size (Debussche and Isenmann, 1989). However, the structure and not just the size of fruits influences feeding visits by various frugivorous birds in New Guinea, with structurally-protected fruits (e.g. capsules) taken almost exclusively by birds of paradise while large, unprotected fruits were consumed by pigeons and bowerbirds (Pratt and Stiles, 1985). A study comparing fruit choice in 25 frugivore species including birds, primates, and small and large ground mammals in Thailand shows that small fruits and large, soft fruits with many small seeds are consumed by a wide spectrum of frugivores, while larger fruits with a single large seed are consumed by few potential dispersers (Kitamura *et al.*, 2002). Moreover, small frugivores that thrive in small and degraded forest fragments in

Southeast Asia are not able to consume these large, single-seed fruits (Kitamura *et al.*, 2002). Large-bodied frugivores are therefore especially important seed dispersers not only because of their ability to swallow large fruits but also because of their long seed retention time, which enables them to move seeds away from parent plants and transport large seeds over long distances (Wotton and Kelly, 2012, Ruxton and Schaefer, 2012, French and Smith, 2005).

Frugivores' consumption of fruit is also determined by their ability to digest certain forms of carbohydrate (Wellmann and Downs, 2009, Delrio and Karasov, 1990), lipids and proteins (Witmer and Van Soest, 1998, Wang and Chen, 2012, Soriano, 2000). Frugivores frequently supplement their predominantly nutrient-dilute (high in water content and low in protein and lipid content) fruit diet with nutrient-dense fruit and insects for activities that go beyond maintenance, such as breeding and migration (Downs, 2008, Smith *et al.*, 2007, Herrera *et al.*, 2006, Boyle, 2010). In a comparison of morphological and chemical fruit traits, it was found that fruit colour more than any fruit trait reflected fruit preference among frugivore assemblages in South Africa and Madagascar (Voigt *et al.*, 2004). Not only fruit nutrient composition and morphology but also frugivore gut morphology or the presence/absence of a gizzard was found to influence the processing of fruit pulp and seeds (Delrio and Restrepo, 1993). Fruit removal and sugar concentration were highest in young secondary forests independent of fruit nutrient concentration (Lumpkin and Boyle, 2009).

Seed dispersal and predation are two of the most important processes regulating the extent and patterns of plant regeneration (Wang and Smith, 2002). Successful reproduction in plants requires the removal of seeds away from the region of highest seed and seedling mortality, which is directly beneath the parent plant (Chapman and Chapman, 1996, Janzen, 1970). The spatial distribution of dispersed seeds around the maternal parent, called the "seed shadow", varies with the mode of dispersal and disperser (Willson and Traveset, 2000). Seed dispersal aids in seed establishment in suitable sites with conditions that improve germination, survival and growth (Schupp *et al.*, 2010, Vander Wall and Beck, 2012). The demographic characteristics and dynamics of plant populations, therefore, are a reflection of the reproductive success of individual plants (Levin *et al.*, 2003). It is also through seed dispersal to suitable sites that plant populations are able to recover from localized extinctions and promote gene flow between populations (Schupp *et al.*, 2010).

The probability of seed deposition (or establishment), however, is decreased by forest fragmentation, owing to the decreased availability of woody perches and fruit-rich edges for seed dispersers (Herrera and Garcia, 2010, Herrera *et al.*, 2011). Large- and medium-gaped birds with predominantly frugivorous diets are less abundant in forest remnants and regrowth, while small-gaped and other birds with mixed diets or fruit as a minor dietary component are most abundant in regrowth (Moran *et al.*, 2004, Moran *et al.*, 2009). Successful seed removal, scatter-hoarding and consumption by rodents decline in small, severely hunted sites in the Atlantic Forest of Brazil, limiting plant recruitment (Galetti *et al.*, 2006). Similarly, bushmeat harvest altered seedling banks by favouring lianas, large seeds, and seeds dispersed by bats, small birds, and wind, probably through the elimination of seed predators (Wright *et al.*, 2007).

1.3.3 Seed predation

Seed predators or species that feed on seeds in fleshy fruits are responsible for pre- and post-dispersal loss of seeds. Pre-dispersal seed predation takes place when fruit or seeds are removed from the parent plant before dispersal, while post-dispersal seed predation happens after seeds have been released from the parent plant. Some examples of seed predators include colombine monkeys and rodents among the mammals, and parrots, pigeons, and finches among the birds (Corlett, 1998, Janzen, 1981, Lambert, 1989).

In one study in Mexico, up to 56% pre-dispersal loss of seed production could be attributed to Lilac-crowned Parrots *Amazona finschi*, a greater rate than post-dispersal removal by vertebrates (51%) or insects (36%) (Villaseñor-Sanchez *et al.*, 2010). In another study in Peru, Peruvian red uakaris *Cacajao calvus ucayalii*, a primate, ate 55.4% seeds, 38.9% pulps and arils, and 5.6% other items in varying proportions throughout the year (Bowler and Bodmer, 2011). Seed predation can be beneficial as in the case of exotic pine predation in a forested site in Patagonia, Argentina, which reduced the chances of exotic seed establishment and helped maintain native tree formations (Nunez *et al.*, 2008).

Scatter-hoarding rodents in the Old World use seed size in their choice between seed predation and dispersal, with small seeds consumed in situ and medium-sized to bigger seeds removed or transported farther away (Wang and Chen, 2009, Wang *et al.*, 2012). Similarly, Xiao *et al.* (2005) found that dispersal distances (including mean, maximum and distribution range) of seeds in primary caches and of seeds eaten after dispersal significantly increased with seed size. Larger seeds were also re-cached more often than smaller ones, which reduced relative density among caches and extended dispersal distances (Xiao *et al.*, 2005). However, a study of post-dispersal seed predation by rodents of 40 tree species in Indonesia showed conflicting results, with predation rates negatively associated with seed size and with thickness and hardness of the seed coat, which may be partially explained by the scarcity of predators capable of penetrating large seeds with hard seed coats (Blate *et al.*, 1998). Moreover, the study found that predation rates were not associated with species' natural dispersal mode (clumped vs scatter-dispersed). This is supported by the work of Moles *et al.* (2003), who compared the survivorship of large and small seeds at the stages of pre- and post-dispersal seed predation. The study did not find significantly lower pre- or post-dispersal survivorship for large seeds compared to small seeds (Moles *et al.*, 2003).

A study found direct positive relationship between tree cover and fruit abundance on species richness and abundance of avian seed dispersers but no effect for fruit predators (Albrecht *et al.*, 2012). This caused seed dispersers to dominate fruit removal in fruit-rich sites accordingly with the dispersal/predation ratio favouring predation in fruit-poor habitat. In contrast, a negative correlation between predation rates and seed production was observed in an avian seed predator in Neuquen Province, Argentina (Shepherd *et al.*, 2008). In years with high seed production, predation rate by Austral Parakeets *Enicognathus ferrugineus* ranged from 0.6 to 3.3% while it was 13.0 to 20.6% when it was low.

Seed predation may show a strong spatial and temporal pattern, with a higher incidence in forest gaps compared to adjacent forest (Boman and Casper, 1995). Similarly, seed predation rates were found to be higher in unconnected forest patches surrounded by degraded, structurally contrasted pastures than in connected ones surrounded by little-disturbed mature forest in Spain (Herrera *et al.*, 2011). In the Neotropics, however, seed dispersal and predation remained constant between secondary and primary forest, although the small-rodent seed predation rate and proportion of seed destroyed were higher than those of large mammals (DeMattia *et al.*, 2004).

Some of the seeds that seed predators consume survive passage through the alimentary canal and are dispersed in the surrounding environment. Black Rats *Rattus rattus* in Hawaii dispersed a portion of the seeds they consumed which passed intact through their digestive tracts (Shiels and Drake, 2011). In the same way, the Chaffinch *Fringilla coelebs*, a typical seed predator, had over a quarter of its droppings containing whole intact seeds that it dispersed (Heleno *et al.*, 2011). Some of Darwin's finches, having predominantly seed predation and insectivory feeding patterns, were found to be capable of endochorous seed dispersal with up to 23% of their faecal samples having intact seeds of which 50% of samples with intact seeds had viable seeds (Guerrero and Tye, 2009). The general tendency is for New World parrots to be wasteful and destructive pre-dispersal seed predators, although they tend to drop uneaten fruit pulp and intact seeds to the ground during feeding bouts which are then scattered by secondary dispersers (Boyes and Perrin, 2010). Astonishingly, the only alpine parrot, the Kea *Nestor notabilis* from New Zealand, consumed more fruit and dispersed more seeds than all other birds in New Zealand combined (Young *et al.*, 2012).

1.3.4 Dispersal ability

Frugivore movement has important ecological consequences on a spatial and temporal scale with a direct influence on seed dispersal patterns. With a diet composed of more than 700 plant species and seed retention time of more than one hour, hornbills are one of the best seed dispersal agents, moving seeds over many kilometres away from parent trees (Kitamura, 2011). Two West African hornbills (*Ceratogymna* spp.) showed wide home ranges of 925-4,472 ha over a one-year period and seed passage time of 51-765 minutes, which translate to seed dispersal distances of 500-3,558 m—with 80% of seeds transported >500 m (Holbrook and Smith, 2000). The same *Ceratogymna* hornbills travel up to 290 km in search of food, which provide evidence that the species are able to map and track available fruit resources in space and time (Kinnaird *et al.*, 1996, Whitney and Smith, 1998, Holbrook *et al.*, 2002). Cassowaries in Australia feed on 238 fleshy-fruit plants with seed retention time of 309 minutes for some species and average seed dispersal distance of 239 m—4% of which are dispersed further than 1,000 m (Westcott *et al.*, 2005). Supra-canopy flight activity was found to be higher among large-bodied parrots and pigeons compared to smaller species at a forested hillside in Papua New Guinea (Symes and Marsden, 2007).

In fragmented and human-altered landscape, frugivore movement is significantly restricted by landscape connectivity and fruit abundance and availability. Toucan movement in southern Mexico was determined by fruit abundance and distances between forest remnants, and not necessarily by the size/area of remnants (Graham, 2001). In a study of avian and mammal frugivores in the Amazon, population density and foraging behaviour of individual frugivores, as well as species composition of frugivore communities, were influenced by fruit abundance (Moegenburg and Levey, 2003). Similarly, abundance and movement of columbids in the Caribbean followed seasonal fruit abundance (Strong and Johnson, 2001). Reserves were of particular importance to parrots in Brazil, as flight activity was highest nearer reserves and forest areas and declined or was absent in anthropogenic habitat where resources were perhaps more limited (Evans *et al.*, 2005). Parrots require undisturbed forest to breed and thrive, as their young tend to stay in nest valleys until they are ≥ 5 months old by which time they learn flight and feeding skills as well as movement patterns from their parents before gradually integrating into adult groups (Myers and Vaughan, 2004, Lindsey *et al.*, 1991).

A complex system of long-distance seed dispersal is through diplochory, a secondary seed dispersal method where a bird of prey feeds on a frugivorous species (e.g. animal frugivores or invertebrates) and increases the distance to which seeds are dispersed (Padilla and Nogales, 2009). These secondary dispersal events were studied more extensively in island ecosystems and were observed in *Falco* sp. and shrike *Lanius* sp. feeding on frugivorous lizards *Gallotia* sp. in the Canary Islands (Nogales *et al.*, 2007, Gonzalez-Castro *et al.*, 2012). It is not hard to conceive that with higher raptor diversity in continental systems, diplochory may occur far more often than observed or recorded.

The Philippines alone has 39 species of raptors, not including new species and recent splits from the Philippine Hawk-owl complex *Ninox philippensis* (Rasmussen *et al.*, 2012).

1.3.5 Diets and dietary breadth

Frugivores are species with fleshy fruits as their main diet or, by common definition, those that have diets composed of >50% fleshy fruits (Fleming *et al.*, 1987). Other dietary components include fish, terrestrial invertebrates, nectar, aquatic invertebrates, plant material other than fleshy fruits, carrion, seeds and vertebrates (Kissling *et al.*, 2009). Several levels of frugivory exist based on dietary breadth or the range of dietary components in a species' diet, including obligate frugivores (i.e. species which exclusively feed on fleshy fruits), partial frugivores (i.e. species with fruits as the main diet but with one or two other dietary components), opportunistic frugivores (i.e. species with fruits as supplementary diet and more than two other dietary components) and non-frugivores (i.e. species with no fruit in their diet) (Kissling *et al.*, 2007). Obligate frugivores are found only in the tropics, whereas frugivores with other dietary components have distributions that extend to extratropical latitudes (Kissling *et al.*, 2009). Partial frugivores occur in low numbers at temperate latitudes but otherwise have similar geographical distributions as obligate frugivores, while opportunistic frugivores and non frugivores are species-rich in the Himalayan foothills, East African mountains and the Atlantic Forest of Brazil (Kissling *et al.*, 2009).

Geophagy, the habit of consuming soil, has been recorded in psittacids, columbids, cracids, and reptilian, amphibian and mammalian frugivores, and is believed to serve to aid in the mechanical breakdown of food and digestion, adsorbing dietary toxins or supplementing mineral requirements (Brightsmith and Munoz-Najar, 2004, Johns and Duquette, 1991, Sokol, 1971, Kyle, 2001, Downs, 2006, Diamond *et al.*, 1999).

1.3.6 Breeding ecology

Parrots and hornbills are predominantly monogamous breeders that nest in tree cavities, with a few species atypically nesting in burrows dug in cliffs, banks or the ground, and existing cavities in rocks (Collar, 1997, Kemp, 1995). Monk Parrots *Myiopsitta monachus* build communal nests in trees (Eberhard, 1998), Ground Parrots *Pezoporus wallicus* in Australia and the Kakapo *Strigops habroptilus* in New Zealand make burrows in the ground (McFarland, 1991, Powlesland *et al.*, 1992), Yellow-faced Parrots *Alipiopsitta xanthops* lay eggs in cavities inside termite mounds (Dias, 2011) and the Guaiabero *Bolbopsittacus lunulatus* in the Philippines makes nests inside wasp nests (Rosell II *et al.*, 2007). The features of nest sites, such as nest height, tree diameter, nest spacing, status of nest tree (living or dead), and nest hole characteristics (e.g. cavity dimensions and orientation), vary considerably with species and geographical location (Forshaw, 1989, Poonswad, 1995, Kemp, 1995). Some species choose dead trees wherein to build cavity nests (Joseph *et al.*, 1991) while others prefer live trees (Datta and Rawat, 2004). Cockatoos in Sumba, Indonesia, prefer cavities in trees with active nestholes belonging to other birds (Walker *et al.*, 2005). Larger species naturally require larger cavities: thus the smaller Visayan Tarictic Hornbill *Penelopides panini* has smaller cavity dimensions compared to the larger Writhed-billed Hornbill *Aceros waldeni* (Klop *et al.*, 2000). Availability of nestholes limits reproductive output in larger species by increasing competition within and between species as well as with other cavity-nesting bird families (Heinsohn *et al.*, 2003, Symes and Perrin, 2004, Murphy *et al.*, 2003, Renton and Salinas-Melgoza, 2004).

Columbids on the other hand typically build nests on flimsy platforms of twigs and sticks lined with grasses and other plant materials on tree branches or on the ground in treeless areas (Myburgh and Broekhuysen, 1974, Johnsgard, 2009). The breeding behaviour of the Critically Endangered Negros Bleeding-heart *Gallicolumba keayi* was described from Panay island, Philippines as nesting low in epiphytic ferns from March to June with chicks fledging after only 12 days (Slade *et al.*, 2005). Other Philippine bleeding-hearts were observed to have similarly low stick nests at 1-2 m from the ground situated on bushes, epiphytic ferns, horizontal branches of low trees or tangles of vines, and lined with vine tendrils and incorporating leaves, bamboo and greenery (Gibbs *et al.*, 2001). Bleeding-hearts in the Philippines typically lay two eggs except for the Mindoro Bleeding-heart *Gallicolumba platenae* which has only one creamy-white egg (Gibbs *et al.*, 2001, Lastica *et al.*, 2012). The Cream-bellied Fruit-dove *Ptilinopus merrilli* was observed nesting in May and also with a single egg (Gibbs *et al.*, 2001).

The onset of breeding in many frugivorous bird species in the Philippines occurs during the summer or dry months (Dickinson *et al.*, 1991). The dry season is favoured for breeding because adverse weather conditions disrupt nesting behaviour through flooding events (Walker *et al.*, 2005). Fruit abundance limits fruit-pigeon breeding, with scarcity of fruit resulting in delayed onset or failed nesting attempts (Powlesland *et al.*, 1997). Clutch size is from two to eight white eggs for both hornbills and parrots, with smaller species producing more eggs (Kemp, 1995, Klop *et al.*, 2000, Forshaw, 1989), and one to three white eggs for pigeons (Devi and Saikia, 2012, Campbell *et al.*, 2008, Hanane *et al.*, 2011). However, birds in general follow a latitudinal gradient in clutch size with larger clutches in the temperate region compared to the tropics due to the increasing seasonality of resources from the tropics to the poles in combination with decreasing predation rates and/or length of breeding season (Griebeler *et al.*, 2010). Incubation in parrots is usually undertaken by females although the task is shared in several species including cockatoos, with longer incubation periods for larger species (Forshaw, 1989). Before egg-laying and incubation in all hornbills with the exception of ground-hornbills, the female (sometimes assisted by the male) seals the entrance to the nesting cavity with a wall made of mud, droppings and fruit pulp (Kemp, 1995). Males provide food for the female through a narrow slit in the wall of the nest cavity during incubation and the early stages of nestling development (Kauth *et al.*, 1998, Kemp, 1995). Cooperative breeding where conspecifics help the breeding pair raise the young is common in hornbills, rare in parrots and unrecorded in pigeons (Witmer, 1993, Oren and Novaes, 1986, Kinnaird and O'Brien, 2007). The young for both parrots and hornbills receive parental care from three weeks to several months after fledging (Forshaw, 1989, Kemp, 1995).

1.3.7 Habitat tolerance and preferences

Studies have documented the importance of protected habitats for forest frugivores sensitive to human disturbance. Large frugivores in a tropical cloud forest in Costa Rica were moderately tolerant of intermediate but intolerant of severe habitat disturbance, while medium and small frugivores were better able to tolerate forest disturbance (Gomes *et al.*, 2008). Parrot densities were lower in a small lowland Atlantic forest reserve compared to a larger reserve, with threatened species strongly linked to primary forests (Marsden *et al.*, 2000). Rare parrots in a hilly forest site in Papua New Guinea were also strongly associated with lower-altitude mature forests (Marsden and Symes, 2006). However, on the Wallacean islands of Buru and nearby Seram, the parrots preferred open-canopied lowland forests while on the distant island of Sumba parrots preferred closed-canopy forests at higher altitudes (Marsden and Fielding, 1999). Forest fragmentation also affected seed predation rates with isolated or unconnected forest patches in northern Spain having increased rates of seed predation on hawthorn *Crataegus monogyna* compared to connected forest patches, and could result in reduced recruitment rates and consequently plant regeneration processes within unconnected patches (Herrera *et al.*, 2011).

Niche partitioning and resource overlap among pollinator or seed disperser species were assessed to measure biotic specialization, which was found to decrease toward the tropics (Schleuning *et al.*, 2012). The study suggested that decrease in specialization of mutualistic interactions is a response of pollinators and seed dispersers to increasing local and regional plant diversity, which implies a higher tolerance against extinctions in tropical than in temperate communities (Schleuning *et al.*, 2012). Armbruster (2006) found that specialization in pollination ecology across latitude appears to be evolutionarily labile and reversible to less specialized pollination.

1.3.8 Threatened frugivores and correlates of extinction risk

The 2012 Red List assessment for birds estimated that one in eight bird species is threatened with extinction because of small and declining populations or ranges (BirdLife International, 2012). One-third of these threatened birds are in Asia (BirdLife International, 2001). Moreover, the region's non-passerines, especially large-bodied species, were disproportionately threatened due to exploitation and landscape conversion (Collar, 2001). Owens and Bennett (2000) made a review of the ecological basis for extinction risk in birds and found that species with large body size and long generation time, e.g. parrots, hornbills and pigeons, were increasingly at risk through persecution and introduced predators, while those with small body size and habitat specialization were more at risk from habitat loss. Using forest loss data, Brooks *et al.* (1997, 1999) successfully predicted the number of threatened species in Indonesia and the Philippines but the numbers were underestimated in montane birds and mammals. Likewise, commercial logging and forest fragmentation were found to depress species richness in Sundaic lowland forest birds (Lambert and Collar, 2002).

Walker (2007) made a review of threats to pigeons and doves in the world and found that 19% of 304 extant columbid species are threatened with extinction, with 78%

(45) of those threatened being island species. He reported that the Asia, Australasia and Oceania regions support the highest number of columbid species with Indonesia, the Philippines and French Polynesia being especially important countries within this region for columbid conservation because they support 40% of extant species and half of all threatened species (Walker, 2007). The main threats to columbids are habitat loss and fragmentation, hunting for food, and alien predator species (Walker, 2007). In a study of prehistoric Polynesian columbids, Steadman (1997) recorded the extinction of at least 9 species as well as extirpation of island populations of extant species.

The same increase in threatened species can be found in Asian hornbills compared to those in Africa (Kemp, 2001). Apart from two species on mainland Asia, all threatened hornbills are insular, with the Philippines being the country with the highest number threatened (6 out of 9 total species) and the only country with a recorded hornbill taxon extinction—that of the Ticao Tarictic *Penelopides panini ticaensis* (Kemp, 2001).

More than a quarter of all parrots (90 species) in the world are threatened with extinction, of which two-thirds can be found in the following countries: Indonesia, Australia, Brazil, the Philippines, Colombia and Mexico (Collar, 2000). The main threats are habitat destruction (mainly loss of nest-sites), trade, hunting and introduced species—a cause of grave concern as 93% of threatened parrots are forest specialists (Collar, 2000). There is also the highly depauperate information on parrots in the scientific literature due to difficulty in studying parrots which could lead to inappropriate or ineffective species management and conservation (Collar, 1998). Parrots are a challenge to study because of a number of factors: (1) slow reproduction, which also slows data generation, (2) wide ranging behaviour, which makes them difficult to track, (3) unpredictability, which makes planning their study difficult, (4) non-territoriality, which makes individual identification difficult, and (5) highly cryptic colouration and behaviour when perched, which parrots do most of the day (Collar, 1998).

1.4 Threats to frugivores

The major threats to frugivores almost always result from human activities. Hunting, a key threat, has predominantly been for subsistence in the Orient and is focused on pigs, deer, monkeys and other arboreal mammals, plus porcupines and other rodents, but it has been increasingly catering to the regional market in wild animals for the pet trade and for parts in traditional medicine, ornaments, food and raw materials (Corlett, 2007, Wright *et al.*, 2000). This has reduced and in some places eliminated populations of mammalian dispersers of large-seeded fruits (Corlett, 2007). Amazonian mammals suffer the same fate, with population declines due to hunting correlated with a species' intrinsic rate of natural increase, longevity, and generation time (Bodmer *et al.*, 1997). Deforestation through logging and land conversion for agriculture has also resulted in loss of frugivores (Brash, 1987, Brooks *et al.*, 1999, Brooks *et al.*, 2002, Brooks *et al.*, 1997). Habitat alteration and loss also comes from fragmentation, urban expansion and shifting cultivation (Sekercioglu *et al.*, 2004). Increasing land use intensity as evidenced by farmers' dependence on pesticides and fertilizers impoverish farmland biodiversity which in turn affects frugivorous animals (Freemark and Kirk, 2001). These threats sometimes act synergistically and create secondary impacts such as greater access for hunters and the spread of invasive species and diseases (Sodhi *et al.*, 2004a, Sodhi *et al.*, 2004b).

Using the IUCN threats classification scheme, a quick analysis of threats affecting three frugivorous families provides evidence on the prevalence of human activities as the main driver of extinction and extirpation of frugivorous species worldwide (Table 1.3). The threat category 'agriculture and aquaculture', which includes shifting agriculture, wood and pulp plantations, livestock farming and ranching, and marine and freshwater aquaculture, affects the most number of species or at least a quarter from each family. Surprisingly and possibly an artefact of a faulty search engine, the threat category 'biological resource use', which includes harvesting for the bird trade, fails to record any species affected by it although parrots are one of the most sought after species in the worldwide pet trade (Wright *et al.*, 2001). Perhaps as more research on the drivers of species endangerment among frugivores is conducted, a full assessment will reveal more species at risk from wildlife trade.

Table 1.3 Numbers of species per family affected by major threats to birds based on the IUCN Threats Classification Scheme (v. 3.1, June 2012 version) found in http://www.iucnredlist.org/technical-documents/classification-schemes/threats-classification-scheme.

	Columbidae (n=304)	Psittacidae (n=356)	Bucerotidae (n=55)
Residential and commercial development	18 (5.9)	33 (9.3)	4 (7.3)
Agriculture and aquaculture	76 (25.0)	116 (32.6)	22 (40)
Energy production and mining	17 (5.6)	23 (6.5)	3 (5.5)
Transportation and service corridors	6 (2.0)	14 (3.9)	1 (1.8)
Biological resource use	0	0	0
Human intrusions and disturbance	5 (1.6)	1 (0.3)	0
Natural systems modifications	0	0	0
Invasive non-native/alien species/diseases	35 (11.5)	50 (14.0)	3 (5.5)
Pollution	2 (0.7)	5 (1.4)	0
Geological events	0	3 (0.8)	0
Climate change and severe weather	27 (8.9)	61 (17.1)	4 (7.3)
All	104 (34.2)	159 (44.7)	25 (45.5)

1.5 What we know about Philippine parrots and other frugivores

Twenty-six percent of all parrots in the world (96 or 374) are threatened with extinction (IUCN, 2011). The Psittaciformes is also the bird order with the second highest number of threatened species. Although it is an established fact that habitat destruction and direct exploitation are the major reasons for their endangerment, Collar (1998) identified the dearth of biological knowledge, as evidenced by published accounts on parrot biology i.e.

status, diet, breeding and range, as another major hindrance to species conservation initiatives if not largely contributing to ill-targeted species protection and management objectives in the tropics. Parrots' propensity for ranging very far, breeding slowly, and unpredictable, non-territorial and cryptic behaviour has made it a very difficult species group to study and follow in the field (Collar, 2000).

Arguably the same factors contribute to endangerment in Philippine parrots where all species apart from one shared with Sulawesi are endemic. Consequently, the country has seven threatened endemic parrots and none apart from the Philippine Cockatoo has been well studied (Collar, 1998). In his global review of parrot species in 1998, Collar identified the research/knowledge gaps concerning parrots and listed *Prioniturus* and *Loriculus* as genera where breeding data were non-existent. Five of the endemic parrots and 11 endemic/near-endemic pigeons listed in Kennedy *et al.* (2000) lack breeding information. It was only through efforts of amateur birdwatchers and photographers that the nesting behaviour of the relatively abundant and widespread Guaiabero *Bolbopsittacus lunulatus* was documented in 2007 (Rosell II *et al.*, 2007). *Prioniturus* never had a single paper dedicated to it in the period up to 1998 (Collar, 1998) although several papers dealing with *Prioniturus* taxonomy among other species (Collar, 2011, Schweizer *et al.*, 2012) have come out since, bringing the total number of *Prioniturus* species in the Philippines to six, all endemic with three threatened (two IUCN Vulnerable and one IUCN Critically Endangered) and two near threatened (IUCN, 2011).

The depauperate state of knowledge on parrots apparently extends to all Philippine birds, as a Web of Knowledge search on "Philippine bird" articles since 1950 yielded 88 articles of which only 18 were dedicated to bird ecology. Molecular taxonomy and/or biogeography garnered the highest number of articles at 32. Another popular topic was avian parasites and diseases, which had 16 articles. Papers on species management, wildlife trade, bird distribution and even bird-inspired indigenous dance had fewer than ten articles for each topic. The ecological studies include documentation of breeding, diet, frugivory and seed dispersal, habitat association, predation, impacts of disturbance, threats and movements. Six studies were on bird distribution or assemblage (Paguntalan *et al.*, 2011, Paguntalan and Jakosalem, 2008, Relox *et al.*, 2011, Pagaduan and Afuang, 2012, Gomez *et al.*, 2009, Gruezo, 2009). Only three studies have quantified species abundance (Mallari *et al.*, 2011, Vallejo *et al.*, 2009, Lee, 2005) and two papers by the same authors described an improved method of abundance estimation using point transect distance sampling as well as an improved approach to bird-habitat studies (Lee and Marsden, 2008b, Lee and Marsden, 2008a).

From my regular attendance at the Wildlife Conservation Society of the Philippines' annual scientific symposium, I have observed that terrestrial wildlife research in the Philippines in the past two decades has generally involved generating species lists with little or no effort at species abundance estimation. There is undoubtedly much to be gained from having a thorough species list for an area as long as methods of generating such lists are standard or remain the same across time and locality. This allows for a direct comparison of species composition across sites and seasons, especially in gradient or biodiversity monitoring studies involving sites with varying degrees of forest disturbance or landscape feature, e.g. altitude and slope. This, however, is not the norm and I have come across only one biodiversity monitoring programme in the Philippines since I started doing wildlife research more than a decade ago. It is the only institutionalized monitoring scheme for protected areas in the country, designed as a participatory community-based programme where permanent 2 km transects are designated and where quarterly monitoring walks are conducted to generate species lists and numbers (Danielsen *et al.*, 2003, Danielsen *et al.*, 2005, Danielsen *et al.*, 2007). The strength of the method is in its simplicity, low cost, sustainability even with limited external support, and the short time period from data sampling to management action (Danielsen *et al.*, 2003). Then again problems of data standardization or scientific rigour and ensuing ability to detect population and habitat disturbance trends are raised due to the simple sampling methods employed (Danielsen *et al.*, 2005). A complementary approach involving both conventional/professional and locally-based/participatory environmental monitoring schemes is the better approach to ensure higher level conservation management intervention in protected areas (Danielsen *et al.*, 2007).

On a national and regional scale, international conservation organizations have followed a framework for monitoring biodiversity conservation outcomes using the following indicators: (1) the Red List Index, which is the rate at which the number of species in each IUCN Red List category changes, (2) change in protection status of key biodiversity areas (KBA) or an assessment of the percentage of KBAs with formal protection status, (3) change in habitat extent within KBAs in Palawan, Sierra Madre, and Eastern Mindanao Biodiversity Conservation Corridors, and (4) change in fragmentation in the Palawan, Eastern Mindanao, and Sierra Madre Biodiversity Conservation Corridors (Conservation International, 2006). Species, site and landscape conservation priorities/programmes are designed based on this framework, which is underpinned by biodiversity information from taxonomic experts, data providers and IUCN specialist networks in the region. The dearth and low quality of biodiversity information from the region and the Philippines in particular has the potential to significantly misdirect and impede conservation initiatives by taking away limited conservation resources from sites/species urgently needing it.

1.6 Abundance estimation in frugivores

Bird conservation programmes often use change in estimates of population size or density to gauge impacts of habitat loss, pollution or harvesting, assess population viability or extinction risk, and put forward conservation initiatives that will help bird populations. Its importance is such that the IUCN Red List classification scheme has population density as one of its cornerstones (IUCN, 2011).

There are two basic approaches to abundance estimation: calculating actual density estimates (individuals per unit area) and calculating an index of relative abundance (Bibby *et al.*, 1998). To derive total population counts or absolute density, either all the individuals of the population are counted, or density is multiplied by area occupied (Jongman *et al.*, 1995). Species discovery curves, encounter rates, MacKinnon lists, timed species-counts and mist-netting are some of the methods used in generating abundance indices (Bibby *et al.*, 1998). These methods have been used in surveys of frugivores in many areas – especially in monitoring programmes over large areas. In these cases, species lists from one time period are compared to those from another (Bibby *et al.*, 1998). Recent methods include camera-trapping for cryptic and nocturnal animals (Silveira *et al.*, 2003) and occupancy modelling (MacKenzie and Bailey, 2004, Peters *et al.*, 2010).

Density estimation is often seen as more powerful as ideas of numbers of birds are given and allows interpolation and extrapolation in unsurveyed sites (Jongman *et al.*, 1995, Palmer, 1995). The usual way of calculating density is through the use of distance sampling (Buckland *et al.*, 1993), although spot-mapping or territorial mapping (International Bird Census Committee, 1970) and mark-recapture (Cormack, 1964, Lebreton *et al.*, 1992) has been used. Distance sampling involves noting distances of detections to a transect and estimating the abundance of an object from the recorded detections and distances (Thomas *et al.*, 2010). It can be based on line transects or point counts (Marsden, 1999, Anderson *et al.*, 1979). The assumptions are (1) objects on the line or point are detected with certainty, (2) objects are detected before any responsive movement due to observer presence, (3) measurements are exact, and (4) objects are located independently of the line or point (Buckland *et al.*, 2001). There are several problems associated with surveying frugivores and several papers have looked at ways to improve estimates and compared several methods of abundance estimation (Buckland, 2006, Marques *et al.*, 2007, Casagrande and Beissinger, 1997, Marsden, 1999, Buckland *et al.*, 2008, Lee and Marsden, 2012).

1.7 Overall aim/goal of the PhD

Academic aim

To develop cost-effective methods for gathering baseline ecological and socio-economic data to inform conservation measures for little-known species over large geographical areas.

List of objectives

1. To assess the distribution, population densities, local population sizes and broad habitat associations of parrots and other key frugivorous birds on Luzon using ecological field methods and data from community interviews.

2. To build a predictive model of frugivorous bird distribution and population density using habitat/environmental data from sites of known occurrence.

3. To use semi-structured interviews to glean information on the abundance and ecology of parrots, and on relevant aspects of local people's livelihoods and lifestyles.

4. To use the results of 1-4 to make recommendations on: (a) IUCN conservation status for each species, (b) key conservation areas/habitats for each species, and (c) likely impact of exploitation to local parrot populations and its contribution to the livelihoods of local communities.

5. To use the results of 1-4 to develop field and analysis methods for the effective gathering of distribution and abundance information about poorly-known species over large areas.

Chapter 2

ARE POPULATIONS OF LARGE-BODIED AVIAN FRUGIVORES ON LUZON, PHILIPPINES, FACING IMMINENT COLLAPSE?

2.1 ABSTRACT

Avian frugivores across Southeast Asia, and in the Philippines in particular, are seriously threatened owing to massive loss of habitat and direct exploitation through hunting and the pet trade. Their declines may have dire consequences for wider ecological processes, since many frugivores are also seed dispersers. Twenty-five species of pigeons, parrots and hornbills were surveyed using distance sampling along nearly 500 km of line transects at 14 sites across the island of Luzon. I documented surprisingly few reliable disappearances of frugivores from individual forest patches – in fact the present survey and other fieldwork since 2000 have increased the known extent of occurrence of several species. However, Green Racquet-tail *Prioniturus luconensis* has been recorded at only seven out of 29 historic sites in the last ten years; although possibly a function of poor coverage, this may be a real range contraction. Still more alarming was the absence of large parrots from most sites with apparently intact habitat surveyed. Even where present, large parrots exhibited lower densities than related species in similar habitat in Southeast Asia. Multiplying site-specific density estimates by reserve area, I estimated population sizes for species in five reserves selected from the current protected area network. For six species, including four of six parrots, largest populations in any reserve in Luzon numbered <1,000 individuals, and nearly one-third of all populations in reserves were <100. Given differing opinions and evidence on MVP thresholds, I used a range of MVP values to predict the likelihood that frugivore populations will persist in various reserves. At MVPs of 500, frugivore communities in all but 2–3 of the largest reserves are not expected to

survive. Although seed dispersers may fare better than seed predators (large parrots), and many frugivores are good fliers that can disperse between widely separated sites, I express the concern that without stricter species and site protection a major collapse of frugivore communities may occur across Luzon, with serious implications for ecosystem functioning.

2.2 INTRODUCTION

Seed dispersal by frugivores is vitally important in maintaining forest vegetation dynamics and in rehabilitating degraded habitat after human impact, especially in the highly fragmented forests of the Orient (Corlett, 1998). Up to 90% of tree species in tropical rainforests have vertebrate-dispersed seeds (Willson *et al.*, 1990, Whelan *et al.*, 2008). In submontane forest in the central Philippines the figure is around 80%, with mid- and late-successional tree species visited almost exclusively by large avian frugivores such as hornbills and pigeons (Hamann and Curio, 1999). This implies that forest regeneration capacity will decline with the loss or decline of frugivore populations. In places where frugivores are rare or absent, seedling recruitment of animal-dispersed trees is indeed lower, sometimes with substantial loss of plant species richness (da Silva and Tabarelli, 2000, Cordeiro and Howe, 2001, Babweteera and Brown, 2009). Moreover, the future climate-driven range changes of many plant species depend on frugivorous birds and mammals (Corlett, 2009).

Tropical forest disturbance and fragmentation affects avian feeding guilds differently: granivores tend to increase, while woodpeckers, terrestrial and canopy insectivores and larger-bodied frugivores show lower abundances (Lambert and Collar, 2002, Watson *et al.*, 2004, Gray *et al.*, 2007). Vulnerability to extinction after disturbance is also higher in frugivores, particularly large-bodied taxa (Owens and Bennett, 2000, Gomes *et al.*, 2008, Martin and Blackburn, 2010, Sodhi *et al.*, 2010a). Despite the obvious importance of forest loss to frugivore populations, and of frugivores to forest ecology, little research has been done in the Philippines to examine how habitat loss, degradation and fragmentation affect the viability of frugivore assemblages and populations.

Given an exceptionally high endemism (>47% of vertebrates and >76% plants), high density of endemic species (64.7 plants per 100 km^{-2} and 5.7 per 100 km^{-2} for vertebrates) and extensive loss of original habitat (only 7% of old growth forest remains), the Philippine Archipelago is one of the hottest of biodiversity hotspots globally (Myers *et al.*, 2000, Conservation International, 2007). Protected areas cover almost 11% of the Philippines' land area (although IUCN categories I–IV cover only 6%), but their effectiveness in stemming habitat loss and other impacts on wildlife is not apparent (IUCN and UNEP-WCMC, 2010). Consequently, 33% of the country's 181 endemic birds are threatened, the second highest total of any country in Asia (BirdLife International, 2004). Hunting and commercial trade affect respectively 40% and 20% of the country's threatened birds. Frugivorous birds, particularly large-bodied pigeons, parrots and hornbills, are especially heavily exploited and many species are now threatened, even in protected areas (BirdLife International, 2003). Species such as the Philippine cockatoo *Cacatua haematuropygia*, which once occurred on 52 islands in the archipelago, has suffered serious range contraction owing to intensive trapping for the cagebird trade and habitat destruction, and was found on just eight islands in the period 1989–1994 (BirdLife International, 2001).

The study assessed the current state of populations of multiple frugivorous species (pigeons and hornbills as seed dispersers, parrots as heavily exploited and seriously threatened seed predators) across Luzon, the largest island in the Philippines, in order to gauge the chances of long-term survival for individual species and frugivore communities. First, I attempted to detect range contractions by comparing past and current distribution using occurrence data compiled from the published literature and the present field surveys. Then I estimated population densities at a number of key sites and compared them with those of related species elsewhere in Southeast Asia. I then asked whether estimated populations of frugivores in key protected areas were likely to be large enough to remain viable in the long term. The results were discussed in relation to current knowledge on likely minimum viable populations (MVPs) and possible benefits of dispersal between sites to foresee the structure and size of future frugivore communities of Luzon, and to identify key sites for their maintenance.

2.3 METHODS

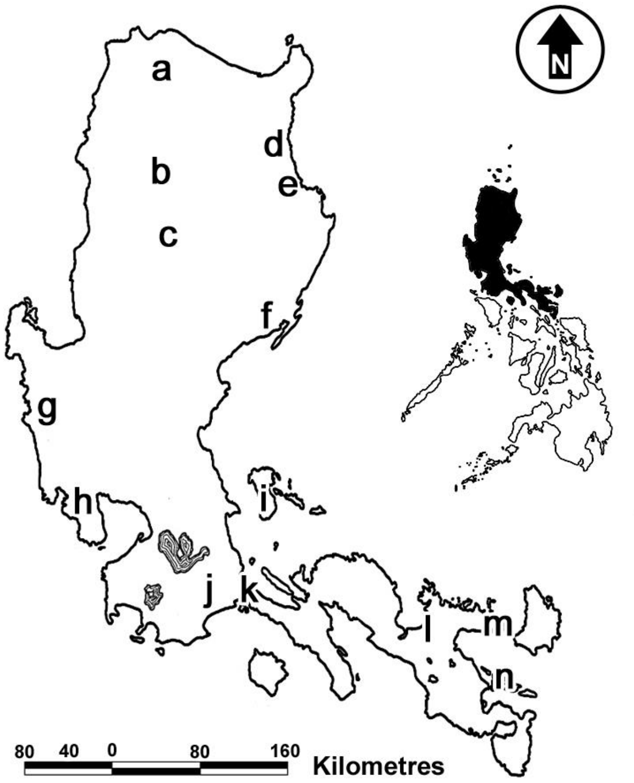
2.3.1 Species distribution

Locality records for 15 pigeon, eight parrot and two hornbill species in Luzon for pre-2000 and 2000–2010 were gathered from the grey literature such as museum catalogues, biological expedition reports, and birdwatching lists (www.birdwatch.ph) to supplement the present surveys (see Appendix 2.3 for site locations and data sources). The distributions of nine selected species (three with IUCN Red List status 'Vulnerable', four 'Near Threatened' and two 'Least Concern' for comparison) were plotted to identify any range contractions due to disappearance from one or more historical sites. These were defined simply as sites where the species was historically but not recently recorded and/or habitat has been so totally lost to urban or agricultural development that their survival is seen as impossible. Confirming disappearance of species from sites is difficult unless they have been intensively sampled. The surveys lasted on average 9 days per site but I augmented field data on species occurrence with informal interviews with local hunters. If local hunters recognised a species from a site, but I did not record it during the bird survey, then it did not qualify as being a disappearance in the species distribution analysis. The Critically Endangered Philippine Cockatoo, which has very few historical records in Luzon and was not encountered in the present survey, was omitted.

2.3.2 Study site and sampling

Surveys for 25 forest frugivores (pigeons, parrots and hornbills) took place on Luzon from December 2009 to September 2010, at 14 sites within five ecologically distinct regions, namely 'Sierra Madre', 'Cordillera', 'West Luzon', 'Central Luzon' and 'South Luzon' (Figure 2.1). These five regions roughly correspond to the subcentres of mammal endemism in Luzon, namely northern Sierra Madre of north-east Luzon, Central Cordillera of northern Luzon, the Zambales mountains of west-central Luzon and Mt Isarog in southern Luzon (Balete *et al.*, 2009).

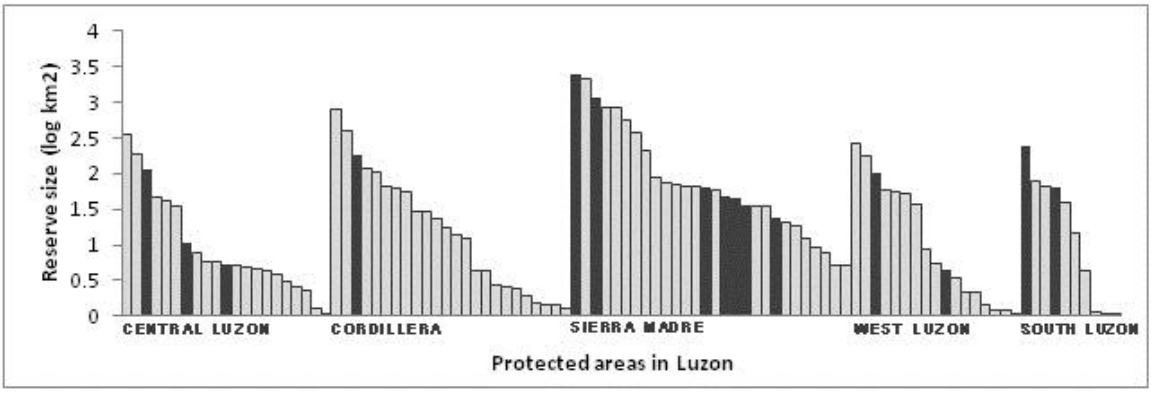
Figure 2.1 Frugivore sampling areas in Luzon. Water bodies are coloured grey on the map. a Calanasan, Apayao (Cordillera); b Balbalasang-Balbalan National Park, Kalinga (Cordillera); c Mt Polis, Cambulo and Pula, Cordillera Administrative Region (Cordillera); d Mt Cetaceo, Peñablanca, Cagayan (Sierra Madre); e Divilacan, Maconacon and San Pablo, Isabela (Sierra Madre); f Baler, San Luis, Dilasag, Casiguran and Dinalungan, Aurora (Sierra Madre); g Mt Tapulao, Zambales (West Luzon); h Subic Watershed Forest Reserve and Bataan National Park, Bataan (West Luzon); i Burdeos, Polillo Island, Quezon (Central Luzon); j Mounts Banahaw-San Cristobal Protected Landscape, Quezon (Central Luzon); k Quezon Protected Landscape, Quezon (Central Luzon); l Mt Isarog National Park, Naga, Camarines Sur (South Luzon); m Caramoan National Park, Camarines Sur (South Luzon); n Mt Malinao, Diaro, Camarines Sur (South Luzon).



Such an extended field season was unavoidable and I acknowledge that birds may have been at different stages of breeding at sites as they were visited. Additionally, it is possible that some species make seasonal short-range or altitudinal movements, although data on such movements are lacking from Luzon. The main currency of bird abundance used was population density derived using distance sampling where 'site' was included as a factorial covariate in detection function modelling. Including site as a covariate works towards accounting for variability in detection across sites which could arise from differences in terrain, habitat or seasonal effects (Buckland *et al.*, 2008). There may also be issues of within-site differences in detectability due to survey timing but I suggest that these are minimal as the number of days between the first and last transects walked at a site was at most 21 days (Subic Watershed Forest Reserve and Bataan National Park; Appendix 2.1). Site-specific population densities are important in formulating species management programmes within reserves.

The total remaining forest cover on Luzon in 2002 was 23.7% (only 8.1% was closed-canopy broadleaf and mossy forest), with cover being greatest in Sierra Madre (35.5% total; 15.7% closed-canopy broadleaf/mossy forest) and lowest in South Luzon (7.7% total; 0.5% closed-canopy broadleaf/mossy forest). The study sites included the largest and third largest reserves in Luzon, and a selection of representatively sized reserves to show the importance of reserve size. There was no significant difference in the proportion of the 50 largest and 50 smallest reserves in Luzon that was sampled ($\chi^2_1 = 2.82$, $p = 0.09$; Figure 2.2) which shows that there was no bias towards any size class in the chosen reserves. All sampling was centred on forested areas, and included the island's three major forest types, cloud forests, pine forests, and mixed dipterocarp forests (Appendix 2.1 which also has details of sampling effort across sites), although transects inevitably passed through areas with varying degrees of disturbance (discussed below).

Figure 2.2 The sizes (log transformed area km²) of the official reserves of Luzon as recognised by the Protected Areas and Wildlife Bureau (Protected Areas and Wildlife Bureau, 2004). Reserves surveyed during the current study are shown in black.



Transect placement in each site was done opportunistically depending on size of site, terrain, and accessibility. Differences in sampling intensity across sites are not seen as a major problem since the currencies of frugivore abundance used (density estimates and encounter rates) take into consideration survey effort. Sites with comparatively low survey effort will have relatively imprecise abundance estimates reflected in wide confidence intervals. There were, in total, 496.8 km of transects across the 14 sites (mean number of transects per site = 15.21 ± 11.42, range = 2–47). Transects mainly followed existing routes, either narrow hunter/farmer trails (80% of total transect length) or motorable tracks (9%) passing through forest reserves; however, in places without human traffic, single-file paths were cut (11%). Within-site transect placement was made with a view to covering as much of the site as possible and to reflect habitat heterogeneity within it. Path width averaged 0.54 m (range 0–6.49 m). Mean transect length was 2.34 km (± 1.38 SD, *n* = 212 transects) and transects were positioned at least 200 m apart. Transects ranged in altitude from 5–1971 m a.s.l. Most traversed forested areas without planted crops (89.1%), but the sample also included agroforestry and forest-edge habitats in foothills and upland farms (10.9% of segments contained some planted crops).

2.3.3 Frugivore survey methods

The survey targeted 15 pigeon, eight parrot and two hornbill species known to occur in forests on Luzon (Dickinson *et al.*, 1991). This set of species are mostly large-bodied but also include the small parrot Colasisi *Loriculus philippensis* while excluding passerine frugivores such as Philippine Fairy-bluebird *Irena cyanogastra* and Philippine Bulbul *Ixos philippinus*. Densities of frugivores were estimated using a line transect distance sampling method (Buckland *et al.*, 2008). The method involved recording all individuals of each target species heard or seen along the transect, and measuring the perpendicular distance of each bird or bird cluster from the transect line (Buckland *et al.*, 2001). Each transect was walked just once. Only perched individuals, or individuals flushed by the recorders, were included in abundance calculations because birds in flight violate the census method assumption that birds are detected at their initial location (Marsden, 1999). The proportions of heard-only records across all species averaged 82.9 ± 15.6% SD and, among species with more than 50 records, ranged from 71.1% in Luzon Tarictic *Penelopides manillae* to 95.2% for Yellow-breasted Fruit-dove *Ptilinopus occipitalis*. A laser rangefinder (Bushnell Sport 450) was used to measure distances but, where the line of sight was obscured, perpendicular distances were estimated to the tree or nearest habitat feature. Transects were walked, one time only, at a standardised pace of 1 km h^{-1}, and only between 0530H and 1100H, and 1500H to 1800H, i.e. when birds are most active (Robbins, 1981). No surveys were conducted in rain, wind or fog as such conditions affect bird activity and detectability (Bibby *et al.*, 2000). I conducted the surveys with 2–5 experienced MSc students and field assistants, all of whom underwent prior training on birdcall identification, distance estimation and habitat assessment. A field guide with bird photos was used to train team members to identify species reliably. The field assistants were indigenous hunters already familiar with birdcalls and with acute distance estimation skills. Distance estimation of both visual and aural detections was checked regularly with exercises to maintain accuracy.

2.3.4 Data analysis

Two of Luzon's parrot species, Philippine Cockatoo and Blue-backed Parrot *Tanygnathus sumatranus*, were not encountered during the survey. Four pigeons in the genera *Geopelia* and *Streptopelia* were excluded from the analysis since they are open country species. The number of frugivore species recorded were summed at each site (observed species richness) but also estimated species richness using the Chao2 estimator in EstimateS v8.2.0 (Colwell *et al.*, 2012) working on the presence or absence of species along each segment of transect at the site. The MCDS (Multiple Covariates Distance Sampling) engine of DISTANCE 6.0 release 2 software (Thomas *et al.*, 2010) was used to estimate species-specific densities (individuals km^{-2}) in individual sites and regions. Bird records were entered as clusters (number of birds in a group/flock) with exact distances rather than distance bins. Right-hand truncation of the furthest 5% of the data was undertaken following Thomas *et al.* (2010), in order to remove those outlying records at large distances away from the transect line which contribute little to the calculated density estimate and hinder model fitting (Buckland *et al.*, 2001). The optimal detection function for each species was selected based on minimisation of Akaike's Information Criterion (AIC) values between models. Site or region was entered as a factorial covariate, depending on the resolution required in the analysis, in an attempt to account for any differences in detection across study areas. These could arise from differences in terrain, habitat, or seasonal effects such that considerable bias could potentially be introduced from changing calling rates, weather pattern, fruiting and therefore food availability across sites (e.g. Buckland *et al.*, 2008). Site-specific population densities hold relevance in formulating species management programmes within reserves. For the four rarer large parrots (*Tanygnathus lucionensis*, *Prioniturus luconensis*, *Prioniturus montanus*, *Prioniturus discurus*), with only 63 records combined from the current survey, data were pooled for the estimation of a common detection probability and species-specific density estimates derived using the multiplier function in DISTANCE.

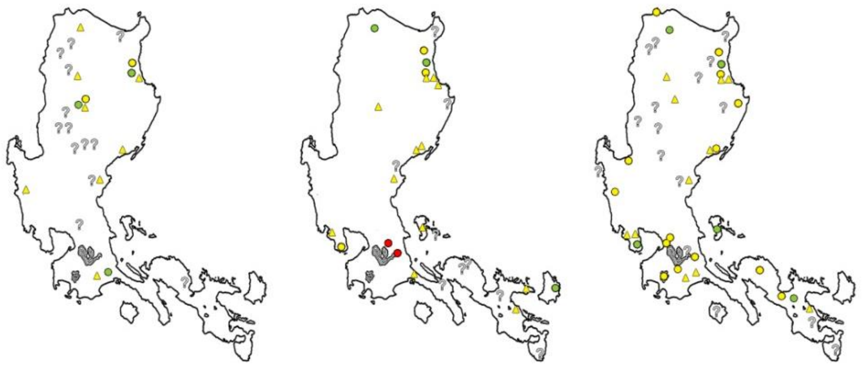
I calculated likely population sizes for frugivores in five protected areas of different sizes, one from each of the five regions (Figure 2.2) as an illustration of the likely sizes of each species' population within a range of reserves (Protected Areas and Wildlife Bureau, 2004). Density estimates in the reserves were calculated based on site-specific density figures and reserve land areas. For each of the protected areas visited during the surveys, I computed the number of seed-dispersing and seed-predating frugivores expected to have populations in excess of three candidate values of MVP. The candidate MVPs used were 5000, 1000 and 500 individuals, the first reflecting the upper 95% confidence interval of MVPs from Traill *et al.* (2007) and the latter two being increasingly 'optimistic' values. The relevance of MVPs is examined more comprehensively in the discussion.

2.4 RESULTS

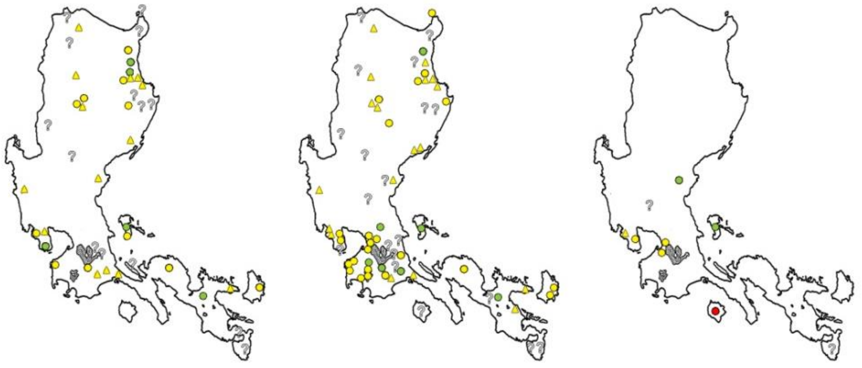
2.4.1 Current and historical distribution of frugivores across Luzon

From the literature review and the current field survey, a total of 89 new (2000–2010) locality records were accumulated, including 18 new sites for the Colasisi, and deduced from them that widespread species like the Colasisi and the Philippine Cuckoo-dove *Macropygia tenuirostris* are likely to maintain a wide distribution in forested sites across Luzon (Figure 2.3). These new records are by no means a reflection of actual range expansions but rather to a large extent an artefact of inadequate past sampling. By contrast, the Blue-naped Parrot *T. lucionensis* appears to have a very narrow range (currently known from six sites), and the Luzon Racquet-tail *P. montanus* may currently be restricted to the northern mountains. Moreover, there is uncertainty whether particular species remain at some localities, especially in areas of the north (Cordillera and Sierra Madre) which have not been visited in the past ten years.

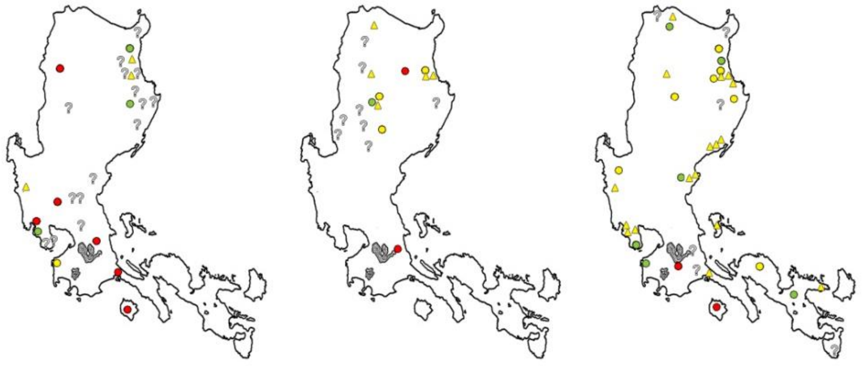
Figure 2.3 Historical (pre-2000) and current (2000 to the present) distribution of key avian frugivores in Luzon, Philippines. Red circle: historical presence in a locality but absence in current surveys; green circle: presence in both historical records and current surveys; yellow circle: new locality records 2000-present; yellow triangle: new localities discovered during the current survey. Localities where a species was recorded historically but have not been visited since 2000 are marked '?'



Ptilinopus marchei (VU) *Ptilinopus merrilli* (NT) *Macropygia tenuirostris* (LC)



Gallicolumba luzonica (NT) *Loriculus philippensis* (LC) *Tanygnathus lucionensis* (VU)



Prioniturus luconensis (VU) *Prioniturus montanus* (NT) *Buceros hydrocorax* (NT)

Five species are likely to have disappeared from 13 sites, in six of which the Green Racquet-tail *P. luconensis* was not found or the site is completely developed now, suggesting that the species is probably locally extinct (Figure 2.3).

2.4.2 Frugivore presence-absence and density estimates at survey sites, 2009–2010

A total of 4372 encounters with 22 target species was made along 496.8 km across the 14 sites. Bataan and Isabela had the greatest observed number of species with 16 each (expected number for Bataan = 17 and for Isabela = 20), while Ifugao in the Cordillera Mountain Range had fewest observed with just eight (estimated = 9; Appendix 2.2). Frugivore communities across the sites were relatively even, with Pielou's Evenness Index (J') exceeding 0.5 for all sites, the lowest being 0.57 for Mt Isarog. The apparent absence of large parrots from most sites was notable (note that absence does not necessarily mean that the species historically occurred in a site). The threatened Green Racquet-tail, for example, was absent from Aurora, a region in which flocks of the bird were recorded by ornithologists and birdwatchers in the early and mid-1990s (F. Danielsen *et al.* unpublished survey report, 1994; T. H. Fisher verbally, 2008). During the survey, the species was encountered on 21 occasions at just four sites, and on just one occasion, a single bird was recorded in the largest reserve in the country. The Blue-naped Parrot was also rarely encountered, with records at Bataan in West Luzon and Polillo in Central Luzon. Blue-crowned Racquet-tail was found in good numbers on the Caramoan peninsula in South Luzon but was not encountered in the Quezon Protected Landscape, a former stronghold (T. H. Fisher verbally, 2008).

Each of the five regions held highest densities of at least one species (Table 2.1). West Luzon had highest densities of six species, Sierra Madre five, Central Luzon four and South Luzon three. Cordillera contained highest density of the Flame-breasted Fruit-dove *Ptilinopus marchei* and the Luzon racquet-tail, both highland species. For parrots only, West Luzon was again the region with highest densities for most species (four of six species). The highest estimated densities were for the White-eared Brown-dove *Phapitreron leucotis* in South Luzon (42.2 km^{-2}; 32.9-54.2 95% CI) and the Guaiabero *Bolbopsittacus lunulatus* in West Luzon (35.6 km^{-2}; 27.7-45.8 95% CI). The highest density for a hornbill concerned the Luzon Tarictic (14.1 km^{-2}; 9.2-21.6 95%CI) in Central Luzon.

Twelve species (four parrots, seven pigeons and one hornbill) never achieved densities over 5 km^{-2} at any site, and four (all parrots) never achieved densities over 3.5 km^{-2} at any site. Overall, 38 of the 50 (non zero) density estimates for pigeons were under 5 km^{-2}, ten of 16 for parrots, and six of ten for hornbills. The proportions of species with density estimates under 5 km^{-2} were no different across pigeons, parrots and hornbills ($\chi^2_2 = 1.34$, $p = 0.51$).

2.4.3 How large are remaining frugivore populations in key reserves?

Only 13 of 22 species (59%; eight of 14 pigeons, three of six parrots, and both hornbills) had estimated populations exceeding 1000 individuals in at least one of the five reserves (Table 2.2). Discounting species that were absent from reserves (NR) and assuming that species present but rare (PR) had very low populations within reserves, 22 (30%) of 73 species-site populations were expected to be lower than 100. No species in Quezon, and just three and four species from Cordillera and Mt Isarog respectively, had populations greater than 500 individuals. Only in Sierra Madre and Bataan did nearly half or more of the species present have populations greater than 500 individuals.

Table 2.1 Density estimates (individuals km^{-2} ± %SE with 95% confidence limits in parentheses) for species in five regions across Luzon, Philippines.

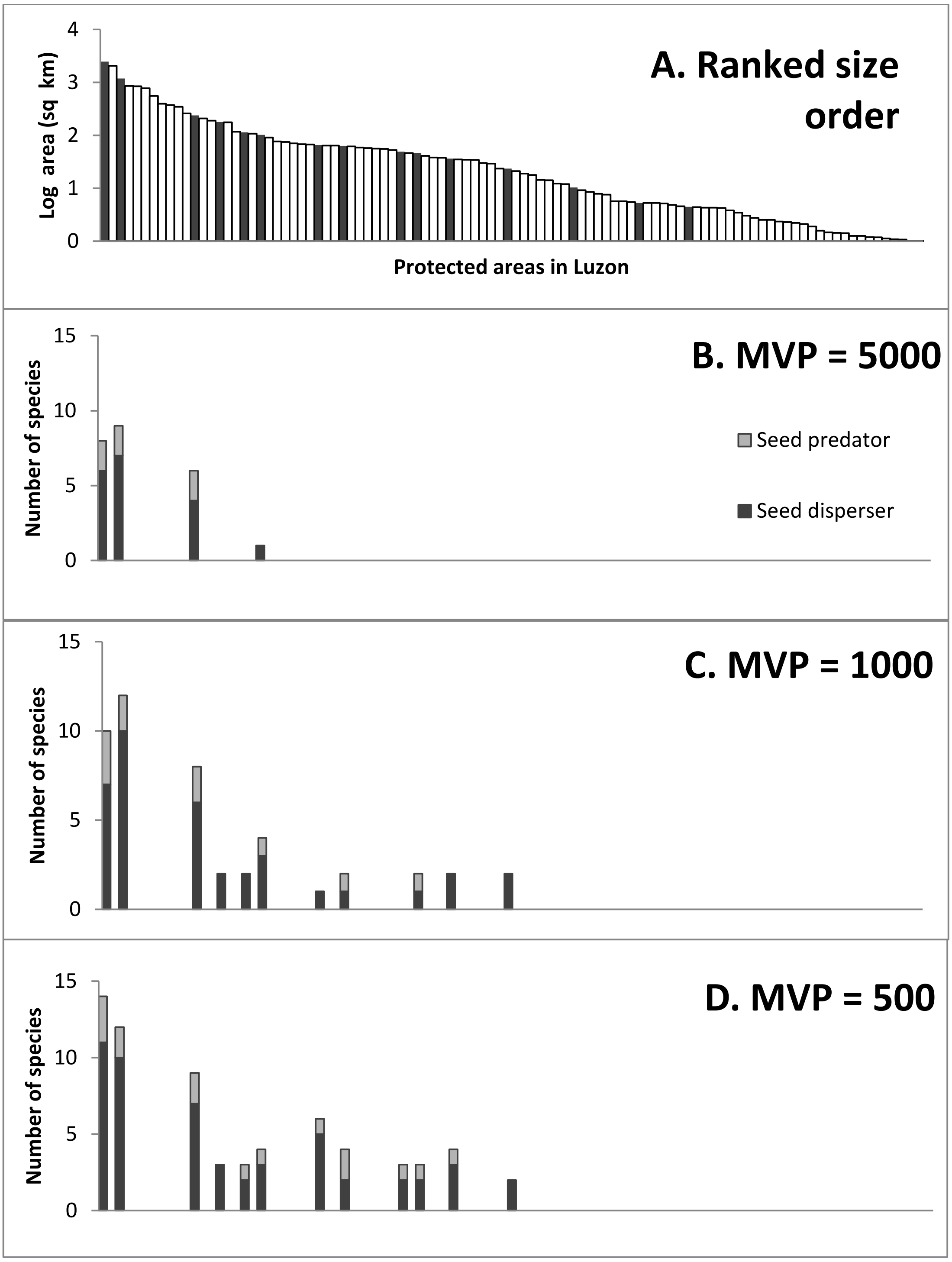
SPECIES	Central Luzon	Cordillera	Sierra Madre	South Luzon	West Luzon
White-eared Brown-dove *Phapitreron leucotis*	20.1 ± 19.8 (13.5-29.9)	5.0 ± 18.8 (3.4-7.4)	29.2 ± 10.7 (23.6-36.1)	42.2 ± 12.1 (32.9-54.2)	22.2 ± 15.5 (16.3-30.3)
Amethyst Brown-dove *Phapitreron amethystina*	4.8 ± 24.5 (2.9-7.8)	3.1 ± 28.0 (1.7-5.4)	15.7 ± 13.1 (12.1-20.3)	2.4 ± 33.7 (1.2-4.7)	2.6 ± 38.8 (1.2-5.5)
Flame-breasted Fruit-dove *Ptilinopus marchei* (VU)	1.3 ± 63.4 (0.4-4.5)	3.5 ± 41.6 (1.5-7.8)	0.5 ± 61.3 (0.2-1.6)	0	0.1 ± 101.6 (0.02-0.5)
Cream-bellied Fruit-dove *Ptilinopus merrilli* (NT)	1.2 ± 41.2 (0.5-2.6)	0.4 ± 49.5 (0.2-1.1)	3.1 ± 27.0 (1.8-5.2)	0.5 ± 58.4 (0.2-1.6)	0.1 ± 100 (0.02-0.6)
Yellow-breasted Fruit-dove *Ptilinopus occipitalis*	0.7 ± 56.5 (0.2-2.0)	0.07 ± 102 (0.01-0.4)	3.9 ± 24.4 (2.4-6.3)	3.4 ± 30.31 (1.9-6.3)	8.4 ± 28.8 (4.8-14.9)
Black-chinned Fruit-dove *Ptilinopus leclancheri*	2.3 ± 32.9 (1.2-4.4)	0.6 ± 62.1 (0.2-2.1)	1.5 ± 29.6 (0.8-2.7)	0	5.0 ± 29.1 (2.8-8.9)
Pink-bellied Imperial-pigeon *Ducula poliocephala*	0	0	0.06 ± 98.6 (0.01-0.3)	0	0
Spotted Imperial-pigeon *Ducula carola*	0	0	0.2 ± 93.1 (0.03-0.8)	0	0
Green Imperial-pigeon *Ducula aenea*	1.2 ± 93.7 (0.3-6.0)	0	0.02 ± 120 (0.004-0.2)	1.7 ± 81.0 (0.4-6.9)	0.8 ± 76.8 (0.2-3.0)
Metallic Pigeon *Columba vitiensis*	0	0	0	0.2 ± 121.6 (0.04-1.7)	0
Philippine Cuckoo-dove *6Macropygia tenuirostris*	7.2 ± 36.1 (3.6-14.8)	0.4 ± 39.7 (0.2-0.9)	0.6 ± 32.5 (0.3-1.2)	7.0 ± 42.7 (3.0-16.4)	5.2 ± 31.8 (2.8-9.8)
Common Emerald dove *Chalcophaps indica*	12.2 ± 26.4 (7.2-20.7)	1.2 ± 52.4 (0.4-3.2)	3.2 ± 20.9 (2.1-4.8)	2.2 ± 33.0 (1.2-4.4)	1.9 ± 34.7 (0.9-3.7)
Luzon Bleeding-heart *Gallicolumba luzonica* (NT)	4.8 ± 35.4 (2.4-9.5)	4.2 ± 52.4 (1.6-11.4)	1.8 ± 38.9 (0.9-3.8)	2.9 ± 37.6 (1.4-6.1)	0.3 ± 71.3 (0.1-1.1)
Guaiabero *Bolbopsittacus lunulatus*	2.2 ± 31.0 (1.2-4.1)	0	9.8 ± 15.2 (7.3-13.2)	18.2 ± 21.8 (11.7-28.4)	35.6 ± 12.7 (27.7-45.8)
Blue-naped Parrot *Tanygnathus lucionensis* (VU)	0.2 ± 75.5 (0.05-0.7)	0	0	0	0.9 ± 54.7 (0.3-2.6)
Green Racquet-tail *Prioniturus luconensis* (VU)	0	0	0.04 ± 75.1 (0.01-0.2)	0	1.2 ± 47.1 (0.5-2.9)
Blue-crowned Racquet-tail *Prioniturus discurus*	0	0	0	0.5 ± 64.9 (0.2-1.8)	0
Luzon Racquet-tail *Prioniturus montanus* (NT)	0	3.5 ± 56.0 (1.2-10.0)	0.4 ± 84.5 (0.1-1.7)	0	0
Colasisi *Loriculus philippensis*	5.2 ± 33.3 (2.7-10.0)	3.1 ± 30.9 (1.6-5.7)	5.8 ± 19.4 (4.0-8.4)	1.9 ± 43.0 (0.8-4.4)	9.3 ± 19.7 (6.3-13.7)
Luzon Hornbill *Penelopides manillae*	14.1 ± 21.4 (9.2-21.6)	1.0 ± 60.9 (0.3-3.2)	7.6 ± 16.4 (5.5-10.4)	6.4 ± 36.0 (3.1-13.2)	11.7 ± 21.8 (7.6-18.0)
Rufous Hornbill *Buceros hydrocorax* (NT)	0.3 ± 46.8 (0.1-0.7)	1.5 ± 29.7 (0.8-2.7)	3.0 ± 12.0 (2.3-3.8)	0.6 ± 47.6 (0.2-1.6)	0.9 ± 28.4 (0.5-1.6)

Table 2.2 Estimated population sizes of key frugivores in selected sites in Luzon. Density figures were based on site-specific estimates. The species density figures in the Northern Sierra Madre Natural Park are based on the combined density estimates of the Maconacon-San Pablo and Divilacan sites. Likewise, the Subic Bay Forest Reserve and Bataan Natural Park species density figures are from the combined density estimates of the Morong, Orani and Subic Bay sites. Figures in bold are population sizes that exceeded 5000 individuals. NR=not recorded, PR=present but rare.

	Quezon Protected Landscape	Balbalasang-Balbalan National Park	Northern Sierra Madre Natural Park	Mount Isarog Natural Park	Subic Bay Forest Reserve and Bataan Natural Park
Region	Central Luzon	Cordillera	Sierra Madre	South Luzon	West Luzon
Area km^2	9.4	178.4	2879	101.1	481
Habitat quality	Good lowland secondary forest	Extensive montane primary forest	Extensive primary lowland to montane forest	Good secondary forest to montane forest	Logged 20 yrs previously but in good condition
Protection	Volunteer forest guards patrol the park infrequently; hunting occurs along edges	Remoteness and unstable peace and order has discouraged commercial logging	Government-sanctioned and illegal logging mostly along the western edge of the park	Forest guards effective in protecting against logging but hunting not controlled	Forest guards provided by the Subic Bay Metropolitan Authority
Observed species richness	13	11	16	10	16
Treron pompadora	NR	NR	PR	NR	**10,285 (1,037-102,106)**
Phapitreron leucotis	360 (221-584)	842 (398-1,779)	**45,756 (29,604-71,145)**	**5,700 (4,159-7,813)**	**15,178 (8,854-26,755)**
Phapitreron amethystina	81 (32-206)	430 (165-1,119)	**118,327 (83,671-177,946)**	426 (196-925)	4,591 (1,763-12,171)
Ptilinopus marchei (VU)	NR	1,077 (364-3,187)	526 (86-3,215)	NR	NR
Ptilinopus merrilli (NT)	52 (20-137)	NR	**9,194 (4,363-23,104)**	PR	234 (35-1,591)
Ptilinopus occipitalis	80 (2-3,539)	NR	**30,957 (702-1,365,942)**	3,897 (88-171,627)	**5,668 (128-250,552)**
Ptilinopus leclancheri	39 (16-95)	103 (17-614)	552 (94-3,252)	PR	356 (51-2,519)
Ducula poliocephala (VU)	NR	NR	PR	NR	NR
Ducula carola (VU)	NR	NR	PR	NR	NR
Ducula aenea	PR	NR	NR	NR	PR
Columba vitiensis	NR	NR	NR	PR	NR
Macropygia tenuirostris	PR	128 (10-1,651)	689 (50-9,564)	1,444 (116-18,039)	1,759 (137-22,720)
Chalcophaps indica	65 (27-156)	353 (91-1,364)	759 (136-4,223)	301 (107-846)	605 (138-2,654)
Gallicolumba luzonica (NT)	55 (24-127)	1430 (574-3,559)	4,260 (1,554-15,713)	234 (93-591)	193 (29-1,275)
Bolbopsittacus lunulatus	49 (21-115)	NR	**24,164 (12,986-46,984)**	1,935 (1045-3,583)	**31,708 (20,335-50,227)**
Cacatua haematuropygia (CR)	NR	NR	NR	PR	PR
Tanygnathus lucionensis (VU)	NR	NR	NR	NR	PR
Prioniturus luconensis (VU)	NR	NR	246 (42-1,434)	NR	174 (80-380)
Prioniturus montanus (NT)	NR	457 (124-1,680)	1,963 (443-8,698)	NR	NR
Loriculus philippensis	42 (16-111)	299 (93-959)	**28,418 (11,215-72,156)**	121 (27-551)	**6,597 (3,128-14,318)**
Penelopides manillae	303 (212-432)	117 (20-680)	**25,299 (9,997-64,043)**	357 (129-985)	**12,542 (6,411-25,058)**
Buceros hydrocorax (NT)	13 (5-32)	440 (185-1,049)	**11,473 (7,610-19,045)**	PR	696 (231-2,301)

The huge Sierra Madre reserve had the highest estimated populations of 12 out of 16 species (those with at least one population estimate), and the highest number of threatened/Near Threatened species (four). Highest estimated population of three species came from the Subic Watershed Forest Reserve and Bataan Natural Park. The threatened highland Flame-breasted Fruit-dove had highest estimated numbers in Balbalasang-Balbalan Natural Park. At the most conservative MVP estimate of 5000, only four of the surveyed reserves are expected to retain their frugivore assemblages (Figure 2.4). Even at the lowest MVP of 500, only 12 out of 15 reserves are expected to retain their frugivores. The smallest three reserves surveyed had areas < 10 km^2 and held no frugivore species with estimated populations > 500. Looking across the whole reserve network, even at the most conservative estimate of MVP (500 individuals), frugivore communities in all but 2–3 of the largest reserves are predicted to lose high proportions of their frugivore species (Figure 2.4). In fact, of 159 frugivore populations currently extant within the 15 surveyed reserves, only 68 (42.8%) may survive the next 100 years with an MVP of 500. It is important to note that the generic MVP does not distinguish between smaller, faster breeding, and more disturbance-resilient species such as the Colasisi which may have lower MVPs than the ones considered and the larger frugivores (e.g. *Ducula* spp. and *Tanygnathus* spp) with more specific requirements for habitat and breeding whose real MVPs may be higher than those considered here.

Figure 2.4 Numbers of frugivores (seed dispersers and seed predators) with estimated population sizes in excess of three possible minimum viable population (MVP) values (B = 5000 individuals; C = 1000 individuals; D = 500 individuals). A shows the size distribution of all protected areas on Luzon with sites surveyed during this study marked in black.



2.5 DISCUSSION

2.5.1 Frugivore distribution and abundance on Luzon

Comparison of parrot population densities from the current survey with those, also derived using Distance sampling methods, from Papua New Guinea (PNG) and Indonesia reveals that parrots on Luzon are indeed rare. Not a single regional density estimate for any of the large parrot species (*Tanygnathus* and *Prioniturus*; 100–250 g) exceeded 3.5 individual km^{-2} (Table 2.1). In Papua New Guinea (PNG), densities for large-bodied parrots (genera *Eclectus* and *Cacatua*; 350–800 g) averaged 10 km^{-2}, with the two rarest parrots at around 1 km^{-2} (genera *Probosciger* and *Psittrichas*; 550–1000 g). Similarly, density estimates for large parrots (*Prioniturus*, *Eclectus*, *Cacatua* and *Geoffroyus*) in Wallacea, Indonesia were comparatively highest and may be as high as 106 km^{-2} (Marsden, 1998, Marsden, 1999, Walker and Cahill, 2000, Marsden and Symes, 2006). Hornbills in Luzon were also rare, with densities from as low as 0.3–3 km^{-2} for Rufous Hornbill and 1–14.1 km^{-2} for Luzon Tarictic, whereas hornbill densities ranged from 1.3–6.9 km^{-2} for the Sumba Hornbill *Rhyticeros everetti* in Sumba and 25–26 km^{-2} for the Papuan Hornbill *Rhyticeros plicatus* in Seram, Indonesia (Marsden, 1999) and 3–52 km^{-2} for the latter species in PNG (Marsden and Pilgrim, 2003). In Sulawesi, which like Luzon has two hornbill species, densities were again much higher with 9.3–82.7 km^{-2} for Red-knobbed Hornbill *Aceros cassidix* and 18.8 km^{-2} for the Sulawesi Tarictic Hornbill *Penelopides exharatus*. Hornbill densities elsewhere in the Philippines are also much higher, with Palawan Hornbill *Anthracoceros marchei* estimated at 9.6–19.6 km^{-2} in the Puerto Princesa Subterranean River National Park (Mallari *et al.*, 2011). This alarming trend, which may of course extend to other forest species, is not an artefact of sampling placement as only relatively intact habitat were surveyed. There are a number of possible drivers of low density among Luzon's avian frugivores, not least direct exploitation for food and the pet trade (e.g. Pain *et al.,* 2006) and issues related to quantity and quality of remaining forest (e.g. Kastner, 2009; Rickart *et al.*, 2011a).

West Luzon and the Sierra Madre had highest species richness, highest number of threatened/Near Threatened species, and highest population estimates, so these should have highest conservation value for frugivores. The importance of these areas both at the present and in terms of long-term persistence of species can be attributed to their possessing, respectively, the best protected reserve (Subic Bay Forest Reserve) and the largest and most intact reserve (Northern Sierra Madre Natural Park) in Luzon. While it was the US Naval Reservation in the former that maintained Subic's largely intact forest (Posa and Sodhi, 2006), it is the unstable security and remoteness of the latter that has contributed to its protection (Mallari *et al.*, 2001). The risk of extinction is less for frugivores in these two reserves, as indicated by the findings.

The frugivorous birds of Luzon show patchy distributions in terms of both presence and local abundance. Some of this variation across sites is presumably natural, with, for example, Luzon Racquet-tail being confined to the higher altitudes of the Cordillera and Sierra Madre mountains; this species may always have been a northern Luzon endemic. In contrast, the lowland-dwelling Green Racquet-tail, an endemic of Luzon, is now a cause of great conservation concern: first, it has disappeared from a number of localities (largely owing to forest fragmentation and deforestation, as at Mt Arayat, Bucay, and Barit in Abra, and Tanay in Rizal; CPE pers. obs.); second, at sites where it was found it only achieved a maximum density of 1.2 individuals km^{-2}. The absence of *Ducula* pigeons from many sites which retain 'good' forest suggests that frugivores may be under stress (e.g. from hunting) even where habitat remains. While I acknowledge that there is much to learn about the true distribution patterns of Luzon's frugivores and the difficulty of confirming species' absence from sites, a more rigorous evaluation of remaining tropical lowland forests for frugivores in Luzon may reveal further range contraction for these and other lowland species.

2.5.2 Likely population sizes and future viability

The minimum viable population size is the smallest population at which a species is expected to persist in a given length of time (Traill *et al.*, 2010). There is wide variation in estimated MVP from published population viability analyses (PVAs), ranging from 20 individuals to as high as 100,000 (Franklin and Frankham, 1998, Reed *et al.*, 2003, Reed, 2005, Brook *et al.*, 2006, Traill *et al.*, 2007, Traill *et al.*, 2010). However, a standardised analysis using 212 species gave MVP figures of 4169 (3577–5129, 95% CI) with 3742 individuals (2544-5244, 95% CI) specific to birds (Traill *et al.*, 2007). Assessment of population viability in key areas used primarily the threshold of 5000 individuals recommended by several authors (Franklin and Frankham, 1998, Reed, 2005, Traill *et al.*, 2010) as necessary to maintain a genetically robust population within a site. Many frugivores are good dispersers (e.g. Myers & Vaughan, 2004), which in some cases might allow genetic mixing and the rescue of local populations from imminent disappearance (Hanski, 1998). Vulnerability to extinction of frugivore metapopulations at the various sites on Luzon is, of course, unknown, but should depend on several factors including species population sizes in habitat fragments, number of subpopulations in the landscape, species tolerance to disturbance, site isolation and dispersal abilities across what is presumably an increasingly inhospitable matrix (e.g. Moilanen & Hanski, 1998). Isolation may be a more serious threat to frugivore populations in south Luzon given the small size of reserves and a significant human-modified landscape. A less conservative MVP can be applied which is lower than the recommended 5000 MVP value to account for the good gap-crossing abilities of many frugivores (Lees and Peres, 2009, Dexter, 2010).

Although I found little evidence for local extinctions of frugivores from sites in Luzon (Figure 2.3), the MVP evidence suggests that time may be short for some species and areas. Only the Northern Sierra Madre Natural Park (NSMNP), the combined Subic Watershed Forest Reserve and Bataan Natural Park (SWFR-BNP) in West Luzon and Mt Isarog Natural Park in South Luzon had populations that exceeded the MVP and this is true for only eight species across all regions. More than half the species considered may well disappear across all five reserves in 100 years and even the most persistent species may be restricted to just three reserves. All threatened (IUCN Vulnerable) species, i.e. Flame-breasted Fruit-dove *Ptilinopus marchei*, Spotted Imperial-pigeon *Ducula carola*, Pink-bellied Imperial-pigeon *Ducula poliocephala*, Blue-naped Parrot, and Luzon endemic Green Racquet-tail might be lost. Moreover, if I more optimistically peg the threshold at around 1000 individuals (Brook *et al.*, 2006), only an additional two species from NSMNP, SWFR-BNP and Balbalasang-Balbalan National Park (Cordillera) will survive long-term along with three from Mt Isarog National Park (South Luzon). It is possible that no species would be able to persist in the smallest reserve, Quezon Protected Landscape (QPL) in Central Luzon, under either scenario (Figure 2.4), although it may be that loss of some species of frugivores might allow other more resilient species, such as Colasisi or White-eared Brown-dove, to benefit from their loss through reduced competition for some foods.

NSMNP is the single reserve which will be able to sustain the highest number of frugivores (eight species), and the surrounding region of Sierra Madre has the most (28) and largest-sized reserves (covering 9347.78 km^2) in all Luzon. Although West Luzon has the fewest (10) and smallest reserves (covering just 430.51 km^2), it has six of the 'persistent' species (those with populations high enough to be expected to survive) remaining in the SWFR-BNP, the rest of which are found in NSMNP and Mt Isarog

Natural Park. The small size of reserves in South and Central Luzon (they cover only around 750 km^2 within each region), coupled with widespread deforestation in these areas, means that they are unlikely to support viable populations of frugivores (Liu *et al.*, 1993). Verburg *et al.* (2006) assessed connectivity of reserves across Luzon and showed that many in South and Central Luzon suffer from severe fragmentation. Moreover, if NSMNP has the ’threshold’ protected area size capable of supporting the highest number or nearly 50% of frugivores, then all the reserves in Luzon and maybe other islands of the Philippines could be deemed ineffective in the long term.

Rapid species collapse is a reality in many regions of the world (e.g. Sodhi *et al.,* 2004b; Thiollay, 2006; Corlett, 2007). The demise of the Philippine Cockatoo across almost all of its range (BirdLife International, 2001) is a stark example from the Philippines. Certainly, given their very low density estimates and small population sizes in reserves, imminent collapse of populations of many frugivorous and large-bodied species appears likely. It is possible that the recorded declines in and absence of large avian frugivores in many sites in Luzon, as seen in the study, is mirrored in losses of other frugivorous vertebrates such as bats and other mammals due to hunting pressure and/or habitat change (Mickleburgh *et al.*, 2009, Heydon and Bulloh, 1997), although quantitative data are largely lacking from the island. Even the relatively intact NSMNP, which given the evidence here offers the best hope for the most number of frugivores in the long term, is now under serious threat from illegal timber exploitation (van der Ploeg *et al.*, 2011). Local collapse of frugivore communities has serious long-term consequences for seed dispersal and forest regeneration dynamics, forest regeneration and plant species diversity. Although parrots, as also seed predators, contribute little if anything to forest regeneration and most often reduce the fitness of the food tree (Galetti, 1992, Ragusa-Netto, 2005), pigeons and hornbills, by contrast, are among the top seed dispersers in rainforests (Hamann and Curio, 1999, Kitamura, 2011). The disappearance of large avian frugivores would deprive an estimated 60% of late-successional plant species in a Philippine submontane rainforest of all their dispersal agents (Hamann and Curio, 1999). Such a significant loss of seed dispersers at a community level can therefore be expected to do irreversible damage to government reforestation efforts and the ecosystem services that forests provide (CIFOR, 2003, Babweteera and Brown, 2009).

A compounding issue is the lack of basic knowledge on breeding, diet, extent of range, foraging behaviour, and habitat preference of frugivores, as well as ecological research on the factors that influence their abundance and distribution (Collar, 1998). While few if any demographic data are available for Luzon's frugivore species, we can expect large parrots and hornbills to have low reproductive rates (Forshaw and Cooper, 1990, Poonswad *et al.*, 1999), suggesting declines cannot quickly be reversed. Some avian frugivores can travel large distances between forest patches (e.g. Myers & Vaughan, 2004), but how these distances compare with the gaps between Luzon's large reserves, how hospitable the matrix is for frugivores, and how likely birds from tiny local populations are to make such dispersal flights, are unknown. Studies looking at how well frugivorous birds disperse across landscapes, which might involve radio-tracking of individuals, would be important for testing hypotheses at a metapopulation level. Knowledge from such research is vital in informing ecological restoration initiatives by identifying key sites and communities that will benefit most from rehabilitation and conservation action (Fordham and Brook, 2010). Further analysis of the data gathered from the present survey will yield correlates of frugivore densities and habitat preference, and clarify threats to the species. To test the hypothesis that hunting is largely responsible for the decline of many frugivores, comparative studies on sites with different levels of hunting pressure could be carried out, complemented with interviews with local people.

In general, more research is needed on how and whether land adjacent to existing reserves could be rehabilitated as part of the national forest estate, in order to improve the chances that populations of Luzon's frugivores, along with many other important forest species, can persist long-term.

Chapter 3

DRIVERS OF FRUGIVORE COMMUNITY COMPOSITION ACROSS LUZON

3.1 ABSTRACT

The Philippines archipelago comprises islands of different origins, ages, climate and habitat, a situation which is expected to produce a biogeographically complex set of animal and plant communities. Community composition, in terms of presence of species and their abundances is also likely to be influenced by anthropogenic processes. I explored similarities between frugivore communities across 24 sites in Luzon using non-metric multidimensional scaling and attempted to explain site differences in terms of a series of geographical, habitat, and disturbance predictors using Mantel tests. NMDS ordinations based on presence/absence were rather different to those using bird densities. In both cases, clusters and outliers did not seem to ordinate simply according to region. Consistent outliers included three sites in West Luzon and two in Central Luzon, and, in terms of species, several large rare parrots and pigeons. The strongest correlates of site dissimilarity were differences in altitude and several human disturbance measures – path width, secondary forest index, canopy closure and a 'human impact index' (reflecting human pressures and forest management). While Luzon's frugivore communities have been no doubt shaped by natural biogeographical processes, their effects have been largely obscured by anthropogenic environmental degradation.

3.2 INTRODUCTION

The structure and composition of avian assemblages and how they relate to aspects of the environment have been one of the dominant themes of investigation in community ecology (Block and Brennan, 1993, Nekola and White, 1999). Specifically, habitat selection in forest bird communities has given birth to many theoretical and empirical perspectives (Cody, 1985). This interest is also, in part, due to the incredible rate at which humans clear forests through extraction of timber and other forest products, livestock grazing, shifting cultivation, and infrastructure development (Whitmore, 1997, Kahn and McDonald, 1997, Terborgh and Nuñez-Iturri, 2006). This presents a great opportunity to measure the response of communities to anthropogenic landscape changes.

The incredible biodiversity in the Philippines has its origin in the long and complex geologic history dating 30-50 million years ago (Heaney, 1986, Heaney *et al.*, 2005, Heaney and Regalado, 1998, Heaney and Mittermeier, 1997). The archipelago of more than 7,000 islands has a mostly oceanic origin with a few islands arising from continental crust broken off from mainland Asia (Hall, 2002). The first of the islands to appear was northern Luzon which explains the well-defined mountain ranges of the Cordillera and Sierra Madre (Hall, 2002). Luzon, being the oldest geologically, has given rise to diverse habitats including high-elevation forested mountains that have a huge influence on the microclimate in certain regions. The Sierra Madre mountain range in northern Luzon for example has documented lower rainfall (averaging 1,649 mm per annum in the period 1975-2004) in the leeward Cagayan valley to the west of the mountain range while the windward east facing the Pacific Ocean gets more rain (3,534 mm on average in 1975-2004) throughout the year (PAGASA as cited in van Weerd and de Haes 2010). This diversity of habitats and environmental variables has in turn produced a high level of endemism even within the island of Luzon alone, a pattern which is repeated for the entire Philippines.

In the Philippines, forest loss due to logging, mining and slash-and-burn farming as well as direct exploitation for food and the pet trade have been identified as the major threats to endemic birds (BirdLife International, 2003). This and having only 7% of its old-growth closed-canopy forest remaining, has earned the Philippines the title as one of the hottest of biodiversity hotspots in the world (Myers *et al.*, 2000, Conservation International, 2007). While the negative response of frugivore communities to human-induced habitat change is well documented in many tropical forest biomes (e.g. (Gomes *et al.*, 2008, Soh *et al.*, 2006, Anggraini *et al.*, 2000, Lefevre and Rodd, 2009, Neuschulz *et al.*, 2011), there are only a few studies on Philippine frugivores and their tolerance to disturbance that I know of (Rickart *et al.*, 2011a, Brooks *et al.*, 1999, Posa and Sodhi, 2006). Likewise, I have not encountered a study exploring environmental determinants of Philippine frugivore assemblages although a study found that large avian frugivores are important in the seed dispersal of 60% of late-successional tree species in a Philippine sub-montane rainforest (Hamann and Curio, 1999).

In this chapter I assessed community differences in Luzon with the use of ordination and clustering techniques. The analyses identified environmental factors that determine frugivore community composition in terms of presence-absence and density across the island in order to understand in part the underlying factors in disappearance of populations and hopefully direct habitat and species management programmes to reduce extinction risks.

3.3 METHODS

3.3.1 Field methods

Data on the presence and abundance of 21 frugivorous birds were collected in 24 sites in Luzon, Philippines representing five regions: Cordillera, Sierra Madre, western Luzon, central Luzon, and southern Luzon. Details of study sites can be found in Chapter 2, Appendix 2.1. In this chapter I separated the sites that were at least 5 km apart. Mts Banahaw-San Cristobal Protected Landscape (central Luzon) was divided into Tayabas and Dolores—adjoining municipalities within the bounds of the reserve and with differing management practices and degrees of hunting. Sites in Isabela (Sierra Madre) were divided into Divilacan and Maconacon-San Pablo. Aurora (Sierra Madre) sites were divided into six: Amro River, Baler, Calabgan, Casapsapan, San Luis, and Talaytay-Simabahan Talagas which are all within reserves. Mt Tapulao in Zambales (western Luzon) was divided into two sites: Kalamansian and Tanagan-Balawey. Lastly, the combined Subic Watershed Forest Reserve (WFR) and Bataan National Park (western Luzon) was divided into three sites: Subic WFR, Mt Natib in Orani, and Nagbalayong in Morong.

Bird species presence-absence and density measures were obtained using methods described in Section 2.3.3 and Section 2.3.4. Data on forest structure used in this analysis i.e. canopy closure, path width, tree architecture, and basal area were collected from 10x20m plots located alternately to the left and right at the 200m mark of each 400m transect segment. Canopy closure was measured using a concave forest canopy densiometer or spherical densiometer (Suganuma *et al.*, 2008, Engelbrecht and Herz, 2001). Transects were along narrow hunter/farmer trails (80%), old logging roads or farm access roads (9%), and in places without human traffic, specially-cut trails (11%). Tree architecture and diameter at breast height (DBH) were determined for the three largest trees in the habitat plot located in each transect segment (Bibby *et al.*, 1998).

From key informant interviews I created an index of human impact considering three factors: hunting of birds, forest condition and/or degree of disturbance, and habitat management. The index with the categorical ranking or score is reproduced below:

- Hunting of birds

  1 Unobserved or very low incidence
  2 Yearly or seasonal
  3 Quarterly
  4 Monthly
  5 Daily or weekly

- Forest condition and/or degree of disturbance
  1. Old-growth, closed canopy forest
  2. Secondary forest (more than 25 yrs old) and/or non-timber forest product (NTFP) harvesting
  3. Secondary forest (15-25 yrs old) and/or selective logging for home consumption
  4. Secondary forest (1-14 yrs old) and/or small-scale logging for the lumber industry along narrow forest trails
  5. Commercial logging along wide logging roads and/or annual slash-and-burn practiced

- Habitat management
  1. Regular patrol by paid forest guards, logging check-points, large-scale government-supported reforestation initiative
  2. Irregular patrol by paid/volunteer forest guards, irregular monitoring of logging activities, small-scale government-supported reforestation initiative
  3. Insufficient number or untrained forest guards, and/or infrequent or ineffective forest patrol, small-scale local reforestation initiative
  4. Untrained volunteer forest guards, sporadic forest patrol, unsuccessful reforestation programme
  5. No forest guards, and/or non-existent reforestation programme

Key informants are conservation workers, hunters, loggers, upland farmers, and those living in the vicinity of the forest. Interviews were mostly conducted in groups and in informal settings. A questionnaire with photos of the parrots, hornbills and pigeons was used as guide for the semi-structured interviews as described by May (2001). These were intermediate between structured and focused interviews and made use of standard questions but the interviewer was free to probe beyond the answers and thus enter into a dialogue with the interviewee. It allowed respondents to answer more on their own terms than the standardized interview permits and at the same time allowed for greater structure for comparability over that of the focused interview. Data on the direct exploitation of parrots and other birds was gathered from interviews and market surveys (Herrera & Hennessey, 2007). In addition, information on the history of forest disturbance and habitat protection/management at sites was also noted.

3.3.2 Data manipulation and analysis

Frugivore community composition was investigated using non-metric multidimensional scaling (NMDS), an ordination method used to explore similarities within a dataset and to identify clustering (Morgan *et al.*, 1976, McCune and Grace, 2002). To measure the similarity coefficients between sites, a data matrix populated with sites, species and either presence-absence data or density estimates was constructed. The Jaccard similarity index was used for presence-absence measures. Frugivore population density estimates derived using distance sampling (see Chapter 2, section 2.3.3 and 2.3.4) were first standardized by subtracting the density estimate of each species with the mean across sites and dividing this by the standard deviation. Similarity between density measures was defined as their Euclidian distance from each other in a given number of dimensions or axes i.e. 3 in this analysis. Ordination success in NMDS was measured numerically by the stress value, and graphically, by the Shepard diagram (Appendix 3.1). A low stress value indicates a reasonable monotonic relationship between distance and similarity. NMDS was preferred over other ordination techniques because it does not assume linearity of the data and it is also reportedly better than metric analogues at reducing distance relationships among samples into fewer dimensions (McCune and Grace, 2002, Legendre and Legendre, 1998, Kent, 2006, Morgan *et al.*, 1976, Minchin, 1987, Cheng, 2004). All NMDS analyses were performed using the software PAST (Hammer *et al.*, 2001).

I used data on structural variables of the habitat as well as measures of human disturbance in order to identify those environmental features which best explained differences in frugivore communities across sites. These were pooled across transect segments to compute for the mean value for each transect and again averaged across transects within each site. From these, dissimilarity matrices (also called distance or difference matrix) were derived between all pairs of 24 sites with respect to the following predictor variables: altitude, geographical distance, seasonality, observer skill, tree basal area, path width, canopy closure, tree architecture, and human impact. Seasonality and observer skill both refer to the number of days between surveys in any two given sites with the former counting the shortest number of days between surveys while the latter includes the consecutive days in the calendar between surveys from the start of the fieldwork in December 2009. Tree architecture refers to the branching of trees with those starting to branch in the lower half of the tree considered as indicators of disturbed and secondary forests (types B and D). Trees with branching that starts above half the height of the tree are indicators of primary and regenerating forests (types A and C). Dissimilarity matrices for the dependent variables i.e. bird species composition based on presence-absence and density were derived from their axes values (in three-dimensional space) in the NMDS analyses using Euclidean metrics. The square matrices were then analysed for significant associations using simple Mantel's tests (McCune and Grace, 2002) in the software PAST (Hammer *et al.*, 2001). Mantel tests were designed to investigate the relationship between multivariate frugivore community structure and the environmental variables (Mantel, 1967) in a way that is flexible since there are multiple design possibilities. A useful feature of the analysis is its ability to make use of qualitative environmental data which in combination with other standardized environmental data works as a non-parametric multivariate analysis of variance with a randomization design (Diniz-Filho and Bini, 1996).

3.4 RESULTS

3.4.1 Community similarities across sites

Sites were ordinated according to species presence-absences (Fig 3.1) and population densities (Fig 3.2). Figure 3.1 has sites that are scattered in ordination space while Figure 3.2 has more tight clusters and well-defined outliers. The strongest outliers in Figure 3.2 have representatives from each region and are the following: Polillo in the central Luzon;

Tanagan-Balawey (TangnBlwey) and Kalamansian as well as Subic Watershed Forest Reserve (WFR) in western Luzon; San Luis, Cagayan, and Maconacon-San Pablo (MacSnPablo) in the Sierra Madre; Balbalasang-Balbalan National Park (BBNP) in the Cordillera; and Caramoan and Mt Isarog in the southern Luzon. Tanagan-Balawey and Kalamansian which are adjacent sites in western Luzon, separated only by a wide slash-and-burn clearing, ordinated close to each other. There is little congruence between Figure 3.2 and the strongest outliers in Figure 3.1 but Subic WFR and Tanagan-Balawey of western Luzon, Mt Isarog of southern Luzon, and Polillo of central Luzon appear as strong outliers in both the presence-absence and density ordinations. Divilacan and Baler of Sierra Madre, and Polis-Cambulo (PolisCmblo) of the Cordillera are outliers only in the former.

Figures 3.3 and 3.4 are ordinations of species against sites in terms of presence-absence and density data. This time the presence-absence data formed a tight cluster of species while the density ordination was more scattered. The main species driving community dissimilarity across sites and common to both presence-absence and density measures are the Blue-crowned Racquet-tail (PRDI), Luzon Racquet-tail (PRMO), Green Racquet-tail (PRLU), Blue-naped Parrot (TALU), and Spotted Imperial Pigeon (DUCA) and to a lesser degree Flame-breasted Fruit-dove (PTMA) and Green Imperial Pigeon (DUAE). Among the strong outliers in the presence-absence ordination only were Metallic Pigeon (COVI) and Pink-bellied Imperial Pigeon (DUPO) while for the density ordination only it is Philippine Cuckoo-dove (MATE) and Colasisi (LOPH). It is notable that all the rare large parrots and pigeons are the strongest correlates of community dissimilarity. The other important drivers of dissimilarity are the two hornbills Luzon Hornbill (PEMA) and Rufous Hornbill (BUHY).

3.4.2 Correlates of community similarity across sites

Community differences in terms of presence-absence were driven more by geographical factors i.e. altitudinal differences than by anything else (Table 3.1). Presence/absence was also significantly correlated with disturbance indicators—path width, canopy closure, and density of secondary forest trees (tree architecture B) and weakly correlated with geographical distance. Density and presence-absence measures did not share significant correlates of community similarity although the combined measure of human impact—hunting, habitat destruction, and habitat management—came close having significantly high correlation with species density but weak with regard to presence-absence measures. Moreover, dissimilarity across sites in terms of density was also correlated with seasonality (p=0.01) and observer skill (p=0.05) and weakly correlated with density of regenerating forest trees (tree architecture C&D).

Sites driving community differences

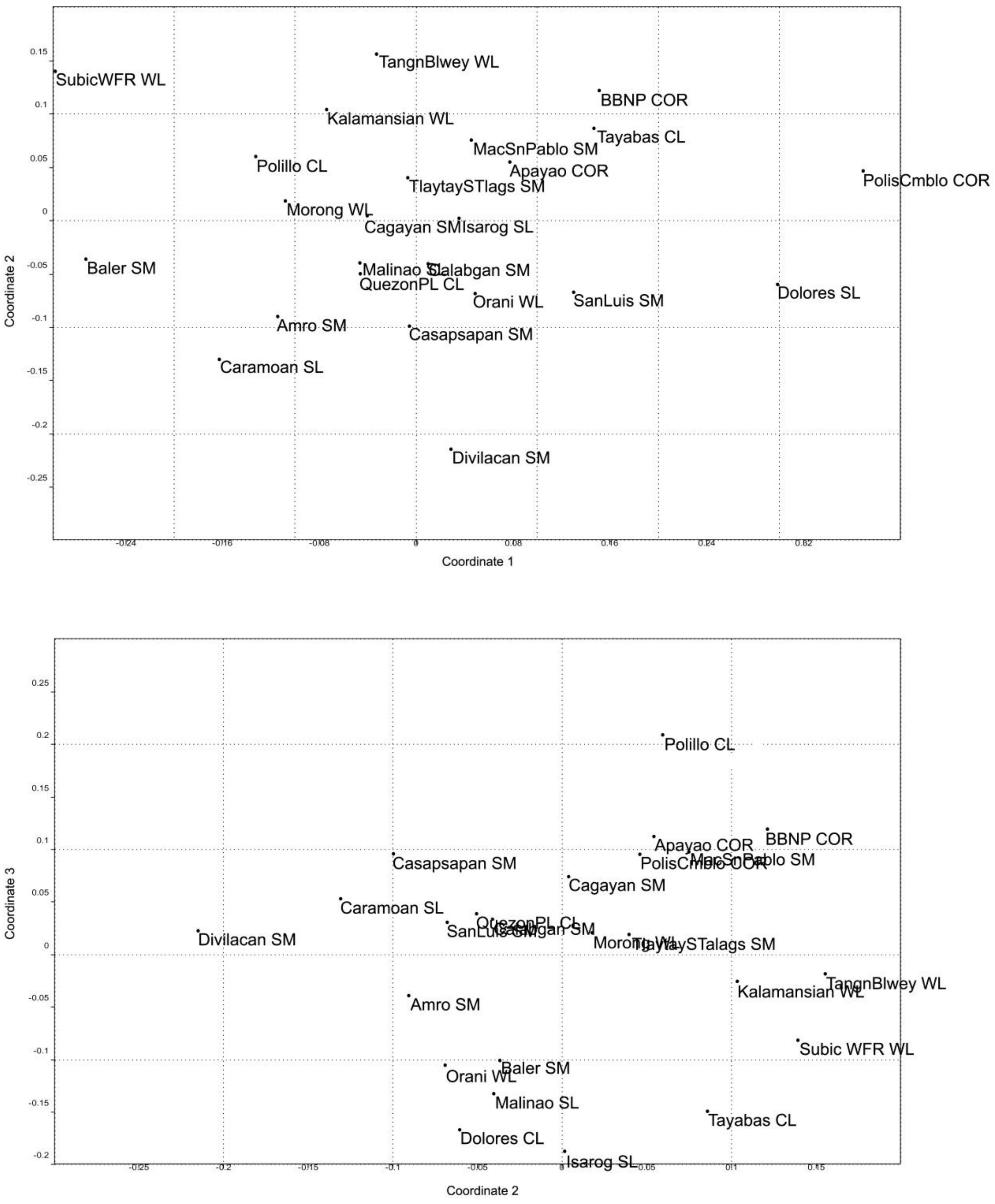


Figure 3.1 Sites ordinated on axis 1 and 2 (top) and 2 and 3 (bottom) of non-metric multi-dimensional scaling (NMDS) based on species presence or absence (Stress = 0.171). The ordination does not show tight clustering of sites and the outliers are not well defined. Site tags indicate the region where a site belongs: CL–Central Luzon, WL–West Luzon, SL–South Luzon, SM–Sierra Madre, COR–Cordillera.

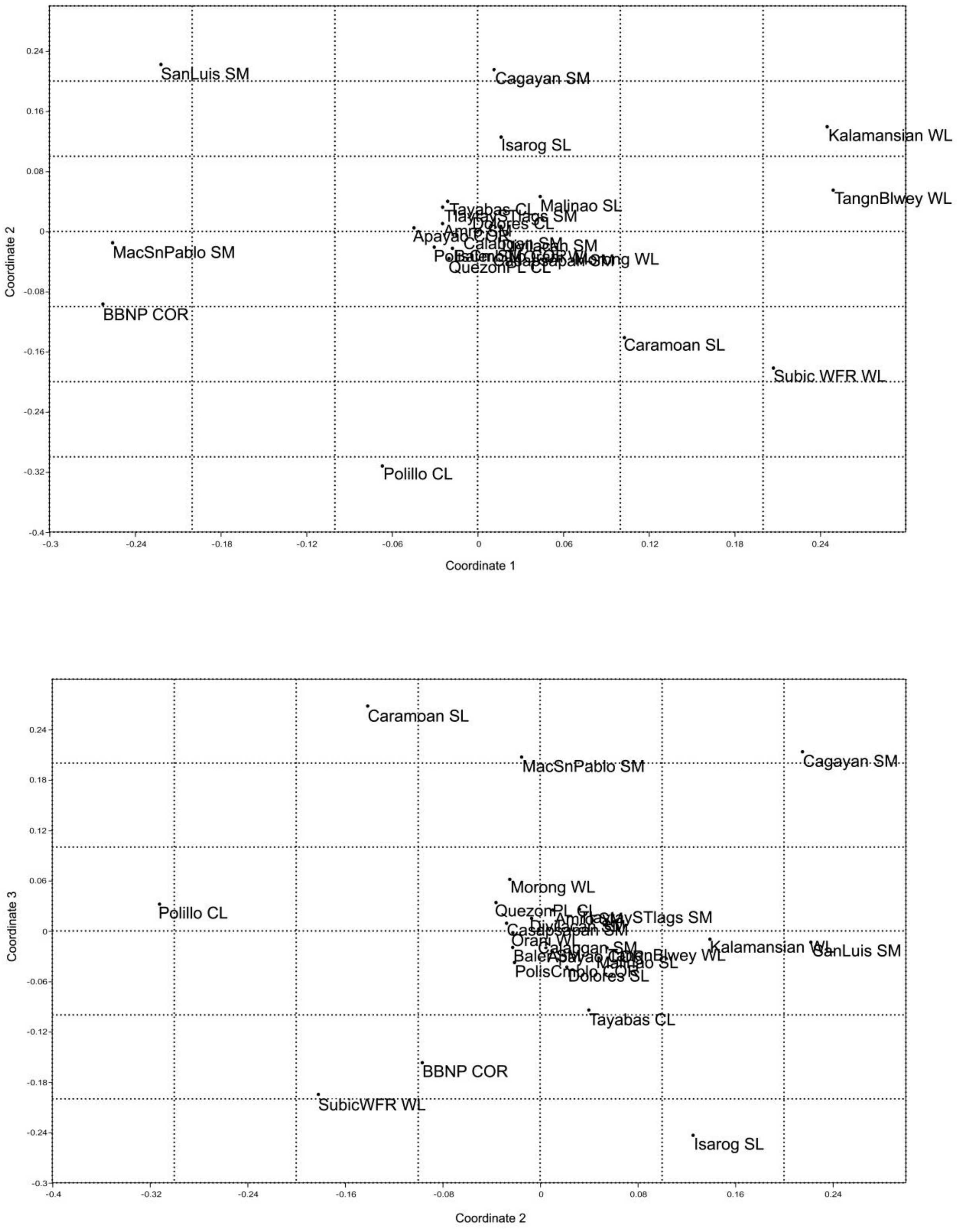


Figure 3.2 Sites ordinated on axis 1 and 2 (top) and 2 and 3 (bottom) of NMDS based on standardised species density (Stress = 0.137). The ordination shows tight clustering of sites with strong outliers from each region including Subic WFR in West Luzon, Caramoan and Mt Isarog in South Luzon, Polillo island in Central Luzon, Cagayan and San Luis in Sierra Madre and BBNP in Cordillera. Site tags indicate the region where a site belongs: CL–Central Luzon, WL–West Luzon, SL–South Luzon, SM–Sierra Madre, COR–Cordillera.

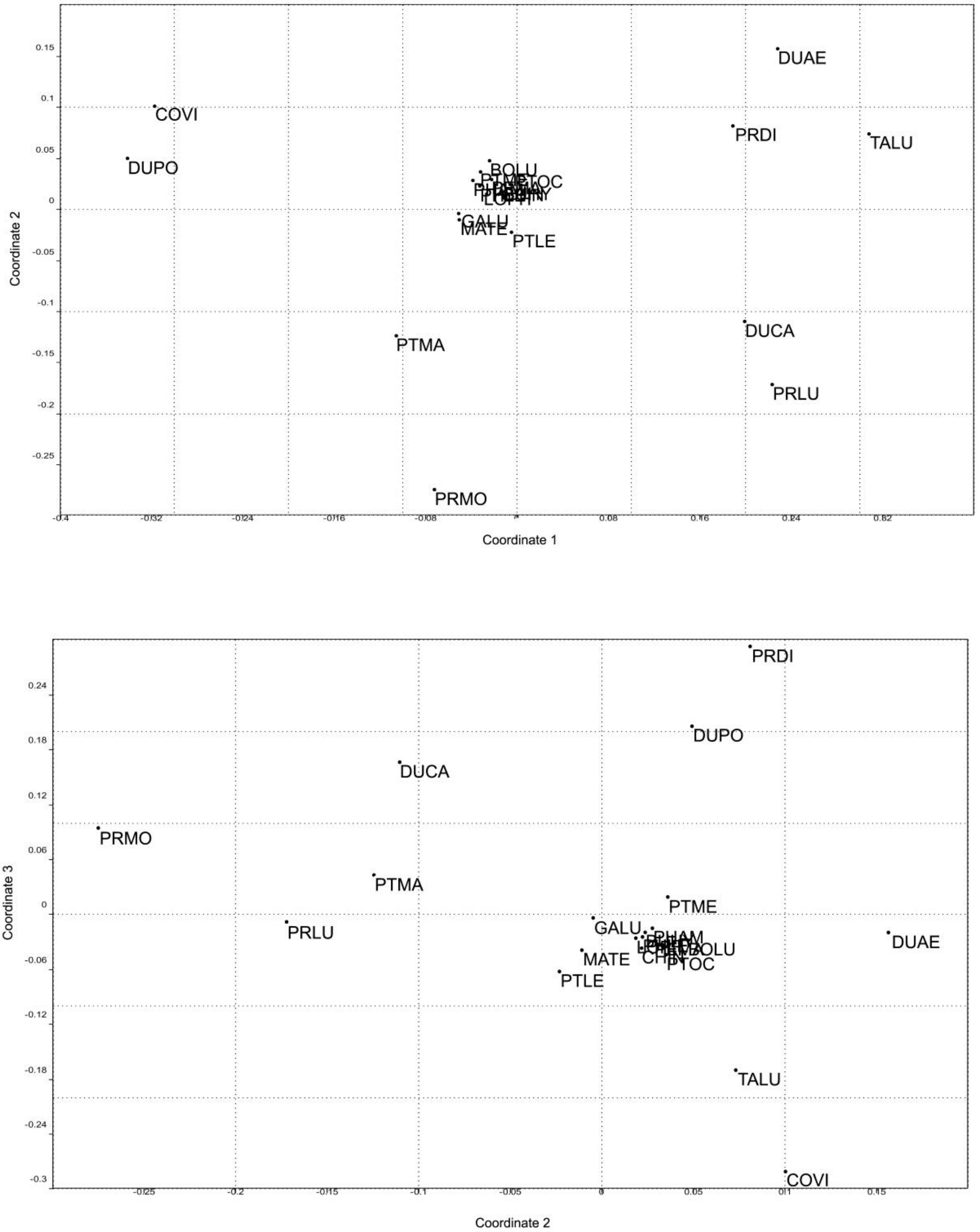


Figure 3.3 Species ordinated on axis 1 and 2 (top) and 2 and 3 (bottom) of NMDS based on species presence or absence (Stress = 0.093). Persistent outliers include PRMO *Prioniturus montanus*, PRLU *Prioniturus luconensis*, PRDI *Prioniturus discurus*, PTMA *Ptilinopus marchesae*, DUCA *Ducula carola*, DUPO *Ducula poliocephala*, DUAE *Ducula aenea*, TALU *Tanygnathus lucionensis* and COVI *Columba vitiensis.*

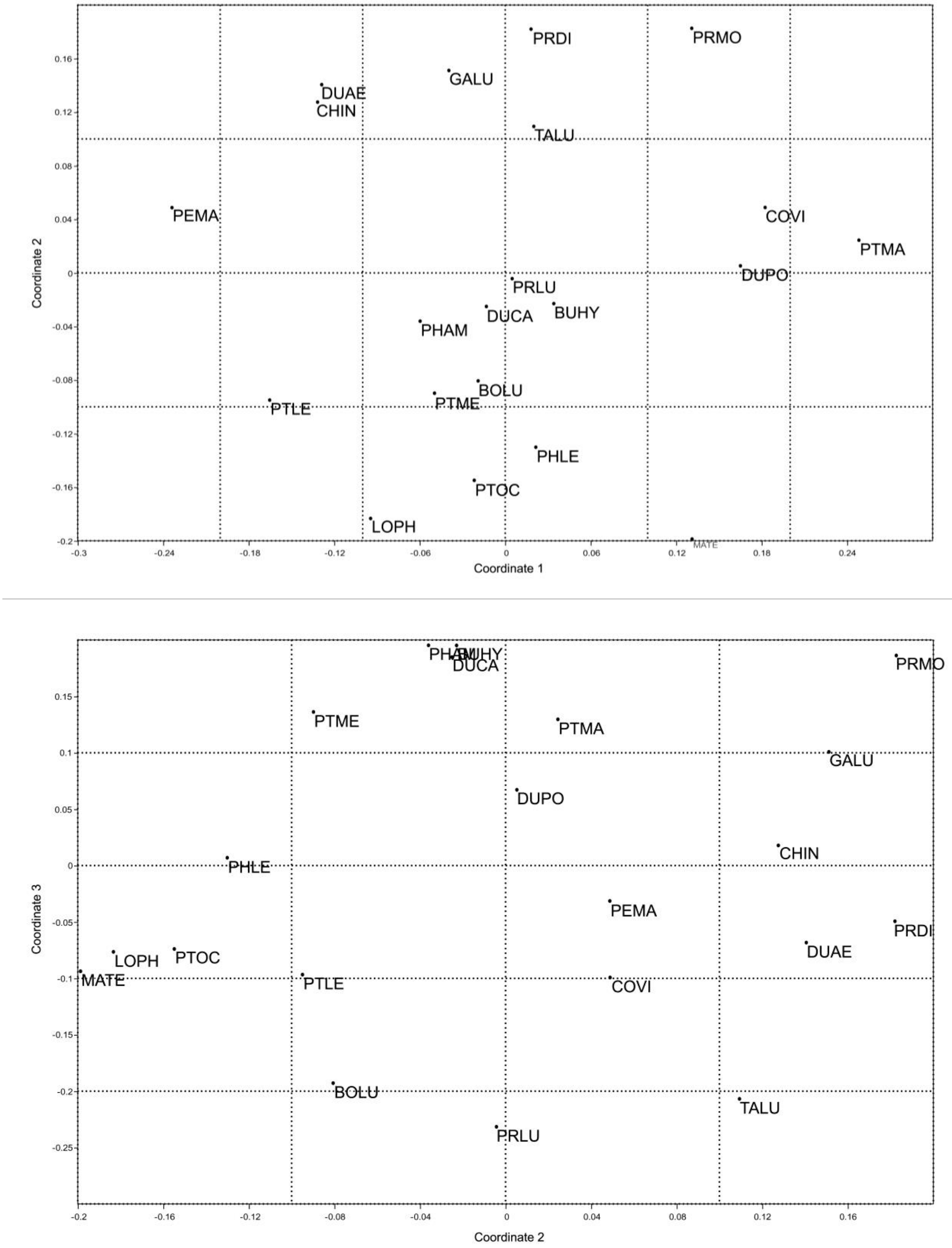


Figure 3.4 Species ordinated on axis 1 and 2 (top) and 2 and 3 (bottom) of NMDS based on standardised species density (Stress = 0.307) showing little or no clustering.

Table 3.1 Results of Mantel correlations between species occurence and density data and environmental correlates across sites in Luzon. Significance are indicated in bold while near significance are italicised.

	Community similarity (presence-absence)	Community similarity (density)
Altitude	**R=+0.51, p<0.001**	R=+0.06, p=0.21
Geographical distance	*R=+0.11, p=0.07*	R=+0.09, p=0.15
Seasonality	R<-0.01, p=0.45	**R=+0.12, p=0.01**
Observer skill	R=-0.03, p=0.65	**R=+0.10, p=0.05**
Basal area	R=-0.10, p=0.88	R=+0.14, p=0.11
Path width	**R=+0.26, p=0.03**	R=-0.19, p=0.87
Canopy closure	**R=+0.14, p=0.03**	R=-0.135, p=0.98
Tree architecture (A)	R=-0.003, p=0.46	R=-0.04, p=0.65
Tree architecture (B)	**R=+0.19, p=0.014**	R=+0.08, p=0.15
Tree architecture (C&D)	R=-0.015, p=0.55	*R=+0.14, p=0.06*
Human impact	*R=+0.10, p=0.08*	**R=+0.22, p=0.01**

3.5 DISCUSSION

Frugivore community composition was not shaped by geographical distance alone but by several factors associated with the differing landscape context as sites across Luzon did not form distinct clusters corresponding to regions in both density and presence-absence measures. Considering density (Fig 3.2), there was a tight cluster of half to more than half of the sites (12-14 of 24) with similar frugivore abundances. This suggests similarity in habitat factors influencing population density in the clustered sites. Conversely, the nebulous configuration of the presence-absence ordination (Fig 3.1) suggests that more complex and varied factors define frugivore assemblage in each site resulting to more pronounced dissimilarity between sites. Sites that were dissimilar in both density and presence-absence measures i.e. Tanagan-Balawey and Subic WFR in western Luzon, Mt Isarog in southern Luzon, and Polillo in central Luzon had highest densities (albeit very small in some) of several species across all sites including some very rare species which were absent in many sites. Geography is commonly identified as a major factor driving differences in animal communities (Qian and Ricklefs, 2012) but Jones *et al.* (2001) pointed to evolutionary development or age of a taxon as a greater influence on species abundance than individual or derived ecological trait. Human alteration of habitats may play a bigger role in species assemblages in the highly fragmented forests in Luzon but to what degree remains unknown.

The three pigeons and four parrot species that were the main drivers of frugivore community dissimilarity share the following traits: large body size, resource specialization, and rarity. These traits were consistently associated with high sensitivity to forest fragmentation with a few exceptions (Renjifo, 1999, Castelletta *et al.*, 2005, Fahrig and Merriam, 1994). Predictably, the widespread fragmentation in the forests of Luzon has resulted in very low densities of large frugivores and their absence in many areas. Several studies have proposed that large-bodied frugivores may be restricted due to their large area requirements and disproportionately affected by hunting (Turner, 1996, Sodhi *et al.*, 2004b, Renjifo, 1999, Brash, 1987). Pigeons, especially large species, and hornbills are hunted for meat in Luzon and there is considerable demand for parrots for commercial trade both in the country and abroad (BirdLife International, 2003, Walker, 2007, Collar, 2000). Rarity, on the other hand, is influenced by a species' ability to disperse through matrix habitats and degree of specialization on resources (Gascon *et al.*, 1999, Sekercioglu, 2002, Henle *et al.*, 2004, Castelletta *et al.*, 2005). The Luzon Racquet-tail, Flame-breasted Fruit-dove and to a degree the Spotted Imperial Pigeon and the Pink-bellied Imperial Piegon were restricted to high-elevation areas, contributing to their rarity and influence on spatial variation of species diversity.

Frugivore species composition in Luzon was strongly correlated with altitudinal differences across sites and abundance of pioneer tree species (with branching below half tree architecture or type B)—a human disturbance measure. Several montane forest specialists e.g. Luzon Racquet-tail and Flame-breasted Fruit-dove may have been responsible for the strong correlation with altitude. The same pattern of community preference for high-altitude habitat can be seen in other taxa with tendency to higher endemism for small non-volant mammals at higher altitudes (Rickart *et al.*, 2011b, Heaney *et al.*, 1989). The remaining correlates of species assemblage were also measures of human disturbance: path width, and canopy closure. Likewise, density measures were also highly correlated with a human impact index which integrates hunting, forest condition and conservation management. The dominance of anthropogenic factors among the significant correlations shows that frugivore composition in Luzon is largely shaped by species' response to human altered landscapes. Many studies have shown that frugivore richness changes in forest fragments compared with continuous forest (Gascon *et al.*, 1999, Cordeiro and Howe, 2001). Frugivore assemblages are also affected by forest fragment size with a direct relationship between fragment size and species richness although the effect is inconsistent as there are cases where an increase in generalist or matrix species was observed following fragmentation (Cordeiro and Howe, 2001, Sekercioglu *et al.*, 2004, Pizo, 1997, Neuschulz *et al.*, 2011). Isolation of forest fragments also affects frugivore assemblage with lower numbers of frugivore species visiting matrix habitats compared to relatively well-forested ones containing certain fruiting plant species favoured by frugivores (Luck and Daily, 2003, Antunes, 2005, Lovejoy *et al.*, 1986).

Seasonality was correlated with species density; a relationship observed in other frugivorous taxon (Galetti, 1997, Verdu and Garcia-Fayos, 1994, Hanya *et al.*, 2011, Ganesh and Davidar, 1999, Klingbeil and Willig, 2010). Variation in species abundances as a response to landscape structure between seasons has been linked to resource abundance and diversity i.e. fruit availability (Ragusa-Netto, 2007, Galetti, 1997). Another way by which seasonality can affect species abundance is in the adverse weather brought about by the seasonal monsoon which is likely to affect species detectability (Robbins, 1981). This has clear implications for conservation monitoring which must be designed to reflect this seasonal variation in species abundances. On the same note, 'observer skill' was correlated with differences between sites in terms of frugivore species densities. In other words, estimates of abundance across sites varied significantly with time from the beginning of the fieldwork that sites were surveyed. In turn, this suggests an improvement in the conduct of field methods by observers over time which has been found to be the case in several studies (Bibby *et al.*, 2000, McLaren and Cadman, 1999). I suggest another reason for the correlation which is the strong winds brought by the northeast monsoon during the start of the fieldwork in late 2009. There are two monsoon seasons in the Philippines, the southwest monsoon (May to October) which coincides with the rainy season and the northeast monsoon (November to March) which brings strong and cold winds (Deppermann, 1954). The strong winds peter out by March which could explain the significant variation in species abundance estimates as previously noted.

Delineation of biogeographical regions was historically based on discontinuities of ecologically relevant attributes of the abiotic environment or vegetation structure (e.g. bioclimatic zones and biomes), discontinuities in the taxonomic composition of assemblages (e.g. zoogeographical realms or floristic kingdoms) or a combination and integration of both (e.g. ecoregions; Kreft and Jetz, 2010). Our results, however, show that the increasing prevalence of human-altered landscapes has so altered species composition that biogeographical boundaries have become obscured (Fig 3.1). It is in such landscapes that the influence of taxon cycle (evolutionary development or age) on species persistence may be seen and/or tested (Jones *et al.*, 2001). A much more dire implication of this is the loss of large frugivores which are the main agents of forest regeneration through their ecological role of seed dispersal (Hamann and Curio, 1999, Moran *et al.*, 2009). This alarming trend of human-induced landscape changes, if continued, will almost certainly lead to changes in community structure, both in terms of the presence of individual species and the densities at which they occur, and in extreme cases, extirpation and maybe even extinction of mostly endemic large frugivore species, creating an environment overrun with widespread species able to colonise and disperse through matrix habitat.

Chapter 4

AVIAN FRUGIVORE HABITAT ASSOCIATIONS ON LUZON

4.1 ABSTRACT

Frugivore populations in many reserves across Luzon have been reduced to such a degree that their future viability has become uncertain. This presents an urgent need to understand better the drivers of species distribution in order to develop appropriate conservation management strategies. To identify habitat associations of 18 avian frugivores, a study was conducted at 24 sites in Luzon, encompassing a total of 1227 habitat plots positioned along 400 m segments of 213 transects. The number of species recorded in each habitat segment as well as the presence/absence of each species was examined in relation to the effects of geographical and vegetation structure and composition using generalised linear mixed models (GLMMs) with site as a random factor. Altitude was the strongest variable correlated with presence of most species (based on Akaike variable weight). Forest disturbance and high-altitude forest were the next strongest variables. Different frugivore species showed unique patterns of association with habitat variables but five species were high-altitude specialists while six preferred lowland sites. Another six species strongly preferred primary forest while one thrives in disturbed forest with the attendant increase in food availability. I then ran generalised additive mixed models (GAMMs) to identify any non-linearities in responses of species to habitat features. Relationships with habitat variables were simple linear or quadratic for the majority of species. Non-linear relationships were rare and found in five species with the variables tree girth and canopy cover. Both structural and floristic variables appear to be important determinants of frugivore composition and should be considered in conservation planning in forest reserves in Luzon.

4.2 INTRODUCTION

Frugivores, with their role as seed dispersers, are crucial to healthy ecosystem functioning through the formation and maintenance of biodiversity (Corlett and Hau, 2000, Kitamura, 2011, Holbrook *et al.*, 2002, Corlett, 2009). While a broad range of animals disperse seeds, birds in particular are credited for dispersal not only in a local but regional or even transcontinental scale (Green *et al.*, 2002, Holbrook *et al.*, 2002). In places where frugivores are absent or scarce, forest regeneration capacity is hampered, sometimes with substantial loss of plant species richness and/or abundance (Moran *et al.*, 2009, Babweteera and Brown, 2010, Neuschulz *et al.*, 2011). Luzon island in the Philippines has seen such an alarming decline in avian frugivore numbers that frugivore population collapse across many including the largest reserves in the island may be inevitable without conservation intervention (see Chapter 2). Knowledge of factors that determine species presence in a landscape underlies every successful biodiversity management and conservation programme (Collinge, 1996, Guedes, 2004, Stagoll *et al.*, 2010, Suchant *et al.*, 2003). Apart from elucidating the nature of the relationship between a bird and its habitat, this knowledge is useful in predicting bird distribution and numbers in unsurveyed sites as well as impacts of land use changes on populations (Bibby *et al.*, 1998, Brooks *et al.*, 1997, Marsden, 1998, Neuschulz *et al.*, 2011, Swift and Hannon, 2010, Marsden *et al.*, 2006). Bird-habitat relationships are complex and research on the subject requires careful characterisation of habitats where species are present and those where they are absent (Lee and Marsden, 2008b). Summary statistics, i.e. median and mean values as well as measures of dispersion, usually precede more complex multivariate analyses. The use of indices is recommended when investigating habitat resource use in proportion to availability (Devictor *et al.*, 2008). When dealing with habitat gradients, e.g. altitude, slope and canopy cover, however, graphical and linear regression approaches are more popular with the exception of species presence/absence data where logistic regression is more appropriate (Bibby *et al.*, 1998, Jongman *et al.*, 1995). Bird-habitat relationships are not always linear and sometimes vary in relationship throughout a year which has implications for fine-scale species management programmes (Meents *et al.*, 1983). Multiple regression approaches are used in detecting non-linear or curvilinear relationships.

I aim here to tie the presence of individual species to habitat and physical features, and to determine the most important drivers of frugivore presence across Luzon. To do this, I first develop multivariate generalised linear mixed models (GLMMs) to identify important habitat features for each species. Then I examine relationships using generalised additive mixed models (GAMMs) to identify non-linearities and thresholds in bird-habitat associations that may help target forest management strategies to conserve key species.

4.3 METHODS

4.3.1 Field methods: bird counts and vegetation measures

Bird and habitat data collection was carried out from December 2009 to September 2010 at 24 sites in Luzon (Fig. 2.1). The sites, which were at least 5 km apart and had a mean distance of 242 km, belong to one of five biogeographical regions in the island: Cordillera, Sierra Madre, western Luzon, central Luzon, and southern Luzon. A detailed description of the study sites can be found in Chapter 2 Appendix 2.1.

Bird species presence/absence was obtained using methods described in Section 2.3.3 and Section 2.3.4. Ten pigeons, six parrots and two hornbills were considered in the current analysis because encounter data were insufficient (less than 9 encounters) for some species of bird and precluded robust analysis. Data on forest structure variables used in this analysis, i.e. altitude, canopy closure, path width and slope, were collected from 10x20m habitat plots located alternately to the left and right of the trail at the 200m mark of each 400m transect segment. Standard tree girths (not less than 30cm) were determined for the three largest trees in the habitat plot (Bibby *et al.*, 1998). Path width along the transect was measured at the 0, 10, and 20m mark of each habitat plot. Canopy closure was measured three times in each plot using a concave forest canopy densiometer. Similarly, slope was measured within each plot using a clinometer at three locations; one along the transect at the 10m mark of each habitat plot and the other two at the opposite corners of the same plot. The average measures of canopy cover, slope, path width, altitude, and tree girth were computed for each plot. The presence of key plants and habitat features which comprise the floristics variables were also noted for each plot. These comprised the following: planted crop, palm, fig *Ficus* sp., dipterocarp, epiphyte, *Parkia javanica*, pioneer tree species, banana *Musa* sp., guava *Psidium guajava*, pandan *Pandanus* sp., tree fern and dead standing tree. These are known or suspected to be an important resource to frugivores. Crops, pioneer tree species, and specific plants i.e. banana and guava are indicators of disturbance and present a possible food source for frugivores. Other known food plants include palm, fig, and pandan. Tree ferns were observed to be used as nesting material of the small parrot Colasisi *Loriculus philippensis* so were included as well. Some such as the presence of epiphytes and dipterocarps are an indicator of good forest with high humidity and closed canopy. Finally, standing dead trees are important for cavity-nesting frugivores such as large parrots and hornbills. Transects were mostly along hunter trails (89%), old logging roads, farm access roads, or occasionally, motorable roads within forested reserves (9%), and specially-cut trails (11%).

4.3.2 Data analysis

Using presence-absence or binary data, the twelve floristics variables were condensed into just three floristics axes (Factors 1 to 3) using PCA or principal components analysis (Jolliffe, 2011). PCA is a multivariate analysis that uses an orthogonal transformation to reduce a number of observed variables into a smaller number of artificial variables called principal components (Jongman *et al.*, 1995). The three axes with the highest eigenvalues were selected as these account for the largest possible variance or variability in the observed variables (Jongman *et al.*, 1995). Multicollinearity, which occurs when two or more predictors in the regression model are correlated, is a potential problem as it increases the standard error of estimates and often yields confusing or misleading results (Zuur *et al.*, 2010, Grewal *et al.*, 2004). To identify multicollinearity among the environmental variables, Spearman's rank correlations were performed on pairs of independent variables using the software PAST (Hammer *et al.*, 2001, Zuur *et al.*, 2010). Since no strong correlations ($r_s > 0.5$) were detected, the analysis proceeded with eight variables; five structural (altitude, slope, path width, tree girth, and canopy cover) and three floristic (PCA Factors 1 to 3).

To investigate the relationship between the presence/absence of frugivores and environmental predictors, I used Generalized Linear Mixed Models (GLMMs) (Bolker *et al.*, 2009) fit by the Laplace approximation with a binomial error distribution, a logit link function, and site as a random factor. Analyses were run using the package 'gamm4' (version 0.1-6) in R (version 2.15.0, R Development Core Team). Models were first developed for each predictor individually, entered both as a linear and as a quadratic term. The five predictor variables with the lowest Akaike Information Criterion (AIC) values were retained and used to build the GLMM models for each species (Burnham *et al.*, 2011). For the Amethyst Brown-dove *Phapitreron amethystinus*, however, the AIC values of the fifth to seventh most ‘powerful’ variables were the same so all seven variables instead of five were used in building the models. The analysis involved a series of iterations using combinations of variables yielding a list of best models with the lowest AIC. Akaike weights, which are a simple transformation of the raw AIC values, were used to quantify the strength of each model in the model set (Burnham and Anderson, 2002, Wagenmakers and Farrell, 2004). Each contributing variable was then ranked according to its strength of influence in frugivore habitat distribution by adding the Akaike weights of models where a particular variable appeared.

Non-linearities in the frugivore-habitat associations were then identified using Generalized Additive Mixed Models (GAMMs) with package ‘gamm4’ in R version 2.15.0 (R Development Core Team, 2012). The predictor variables tree girth, canopy cover, Factor 1 and Factor 2 were chosen for the analyses owing to the fact that they can be manipulated by land managers. The AIC were noted for each model. Finally, I investigated the relationship of species richness in each transect segment with the chosen predictor variables.

4.4 RESULTS

4.4.1 Community analysis

The PCA analysis reduced the 12 binary floristic variables into three axes accounting for 51.5% of variability. PCA axes 1 to 3 (= Factors 1 to 3) described three predominant forest types in the surveyed sites (Table 4.1). Factor 1 describes a mature and rich secondary forest dominated by dipterocarp and palm trees with a thick understorey of tree fern, pandan, figs and epiphytic plants. The habitat was also associated to a lesser degree with standing dead trees and absence of crops. Factor 2 represents disturbed forest or agroforest habitat with crops growing alongside forest trees, in particular fig and pioneer tree species such as *Macaranga* with banana and tree fern in the understorey.

Factor 3 is characteristic of mossy forest in being associated with dense tree fern, and epiphyte growth as well as the absence of dipterocarps, fig and pioneer tree species.

Table 4.1 The three highest scoring factors in the principal components analysis (PCA) of floristic variables. Eigenvalues and percentage variation explained by each factor are shown with the correlations between factor scores and individual variables. Only factor scores greater than 0.2 are shown.

	Factor 1	Factor 2	Factor 3
Eigenvalue	0.392727	0.346379	0.228089
% explained	20.892	18.426	12.133
Correlations with individual variables			
Crops	–0.33	+0.21	(–)
Palms	+0.70	(–)	(–)
Figs	+0.25	+0.78	–0.35
Dipterocarps	+0.68	(–)	–0.47
Epiphytes	+0.59	(–)	+0.31
Leguminous trees	(–)	(–)	(–)
Pioneer trees	(–)	+0.64	–0.21
Tree stump	+0.31	(–)	(+)
Musa spp.	(–)	+0.49	(+)
Guava	(–)	(–)	(+)
Pandanus spp.	+0.29	–0.35	(+)
Tree ferns	+0.45	+0.47	+0.66

4.4.2 Frugivore-habitat associations

Table 4.2 shows the confidence set of variables for each species as well as for frugivore species richness. Floristic variables were correlated with the presence of the highest number of species compared to structural factors. Akaike weights of all predictor variables for each species in Table 4.3 indicate that altitude is the most powerful variable, being significantly correlated with the presence/absence of 12 out of 18 frugivore species and with the highest Akaike weights for ten of these. This is followed by Factor 2 and Factor 3 with 12 species each and garnering the highest Akaike weights for three and two species respectively. Factor 1 was correlated with the presence/absence of 15 species, the highest in total, but did not have the highest Akaike weight for any variable. Four of the variables, altitude, path width, canopy cover and tree girth, behaved in an entirely linear fashion across all species. The remaining six variables had a mix of linear and quadratic relationships with frugivore presence/absence. Factor 3, however, was associated with mid-range values for most species.

The top five habitat features driving species richness at sites were flat slope, big tree girth, and increasing measures of Factors 1 to 3. At the species level, three species, all rare or uncommon, showed entirely linear relationships with variables. One was Green Racquet-tail *Prioniturus luconensis*, which was associated with increasing forest quality and slope, and negatively associated with increasing altitude, canopy cover and forest disturbance. The same variables were important for the Green Imperial-pigeon *Ducula aenea*, which was associated with low altitude, slope and narrow paths, and increased tree girth and canopy cover. Conversely, Blue-crowned Racquet-tail *Prioniturus discurus* was negatively associated with increased measures of good forest and preferred wide forest paths.

The lowland species White-eared Brown-dove *Phapitreron leucotis* and Common Emerald Dove *Chalcophaps indica* were associated with the same variables except for one: the former preferred big trees while the latter was averse to floristic indicators of forest disturbance (Factor 2). Similarly, Yellow-breasted Fruit-dove *Ptilinopus occipitalis* and Guaiabero *Bolbopsittacus lunulatus* shared the same variables, having highest correlations with measures of forest disturbance (Factor 2), but differed in just one, with the former associated with wide paths while the latter showed a preference for closed-canopy forest.

The Flame-breasted Fruit-dove *Ptilinopus marchei* and Luzon Racquet-tail *Prioniturus montanus*, known montane or cloud forest specialists (BirdLife International, 2010), as expected were significantly and positively correlated with altitude. Other high-altitude species include the Cream-bellied Fruit-dove *Ptilinopus merrilli*, Philippine Cuckoo-dove *Macropygia tenuirostris*, and to a lesser degree Rufous Hornbill *Buceros hydrocorax*. On the other hand, White-eared Brown-dove, Black-chinned Fruit-dove *Ptilinopus leclancheri*, Common Emerald Dove, Luzon Hornbill *Penelopides manillae*, Green Racquet-tail, and Blue-crowned Racquet-tail showed a strong preference for lowland sites. Species associated with good forest include White-eared Brown-dove, Amethyst Brown-dove, Cream-bellied Fruit-dove, Black-chinned Fruit-dove, Common Emerald Dove *Chalcophaps indica*, Luzon Bleeding-heart *Gallicolumba luzonica*, Green Imperial-pigeon and Colasisi *Loriculus philippensis*. An opportunistic species, Yellow-breasted Fruit-dove *Ptilinopus occipitalis* profits from forest disturbance and subsequent increase in food availability along forest edges.

Table 4.2 Confidence set of variables for each species with full model sets in Appendix 4.1. + and – indicate positive and negative coefficents respectively. * p < 0.05; ** p < 0.005; *** p < 0.0005.

4.2a White-eared Brown-dove *Phapitreron leucotis*

AvAlt	AvCCover	Factor 1	AvPath	AvGirth	AIC	ΔAIC
– ***	+***	– **		+	1320	0
– ***	+***	– **			1321	1
– ***	+***	– **	–	+	1322	2
– ***	+***	– **	–		1322	2
– ***	+***			+	1324	4
– ***	+***				1325	5
– ***	+***		–		1327	7
– ***	+***		–	+	1327	7

4.2b Amethyst Brown-dove *Phapitreron amethystinus*

AvPath	AvGirth	AvSlope	CCover	Factor1	Factor2	Factor3	AIC	ΔAIC
	+**			+*		+*	1084	0
–	+**			+*		+*	1086	2
	+**	–		+*		+*	1086	2
	+**		–	+*		+*	1086	2
	+**			+*	–	+	1086	2
	+**				–		1087	3
	+**					+	1087	3
	+**			+	–		1087	3
	+**				–	+	1087	3
–	+**		–	+*		+*	1087	3

4.2c Cream-bellied Fruit-dove *Ptilinopus merrilli*

AvAlt	AvGirth	Factor 1	Factor 3	AveSlope	AIC	ΔAIC
+**	+**				499.2	0
+**	+**	+			499.8	0.6
+**	+**				499.9	0.7
+**	+*	–			500.2	1.0
+**	+*	+		–	500.8	1.6
+**	+*		–	–	500.8	1.6
+**	+**	+	–		501.2	2.0
+**	+*	+	–	–	502.1	2.9

4.2d Yellow-breasted Fruit-dove *Ptilinopus occipitalis*

Factor 2	AvGirth	AvPath	Factor 1	Factor 3	AIC	ΔAIC
+**					742.4	0
+**	+				742.6	0.2
+**		+			743.0	0.6
+**	+	+			743.1	0.7
+*		+	+		743.3	0.9
+**			+		743.4	1.0
+*	+	+	+		743.4	1.0
+**	+		+		743.5	1.1
+**				+	743.7	1.3
+**	+			+	743.7	1.3

4.2e Black-chinned Fruit-dove *Ptilinopus leclancheri*

AveAlt	AvGirth	Factor 1	AvSlope	Factor 2	AIC	ΔAIC
–**	+**	+*			458.1	0.0
–**	+**	+*	–		458.2	0.1
–**	+**	+*		–	459.4	1.3
–**	+**	+*	–	–	459.5	1.4
–**	+**				461.5	3.4
–**	+**		–		461.6	3.5
–**	+**			–	462.0	3.9
–**	+**		–	–	462.0	3.9
–**	+*		–		463.2	5.1
–**		+*	–	–	464.3	6.2

4.2f Philippine Cuckoo-dove *Macropygia tenuirostris*

AvAlt	AvPath	AvGirth	AvSlope	Factor 3	AIC	ΔAIC
+***	–	+	–		577.8	0
+***		+	–		578	0.2
+***	–		–		578.3	0.5
+***					578.4	0.6
+***			–		578.6	0.8
+***	–	+		+	578.9	1.1
+***	–	+	–	+	579.3	1.5
+***		+*	–	+	579.5	1.7
+***				+	580	2.2
+***	–		–	+	580.5	2.7

4.2g Common Emerald Dove *Chalcophaps indica*

Factor 2	AvAlt	AvPath	CCover	Factor 1	AIC	ΔAIC
	–				640.7	0.0
	–			–	641.0	0.3
–	–				641.3	0.6
–			+		641.4	0.7
	–	–			641.5	0.8
				–	641.6	0.9
–	–			–	641.7	1.0
	–	–		–	641.9	1.2
–					642.1	1.4
–				–	642.2	1.5

4.2h Luzon Bleeding-heart *Gallicolumba luzonica*

AvGirth	Factor 1	Factor 3	AvPath	CCover	AIC	ΔAIC
+	+*	– *			582.8	0.0
+	+*	– *	–		584.3	1.5
	+*	– *			584.5	1.7
+	+	– *		+	584.6	1.8
+*	+				585.7	2.9
+*		–		+	585.8	3.0
	+*	– *	–		585.9	3.1
	+*	– *		+	586.1	3.3
+*		–			586.2	3.4
+	+	– *	–	+	586.2	3.4
+*		–	–		586.5	3.7

4.2i Guaiabero *Bolbopsittacus lunulatus*

Factor 1	Factor 3	AvGirth	CCover	Factor 2	AIC	ΔAIC
+*				– *	1022	0
+*	+			– *	1024	2
+*		+		– *	1024	2
+*			+	– *	1024	2
+*	+	+		– *	1025	3
				– *	1026	4
+*	+		+	– *	1026	4
+*		+	+	– *	1026	4
+*					1027	5
			+	– *	1027	5

4.2j Colasisi *Loriculus philippensis*

Factor 1	AvSlope	AvGirth	Factor 2	Factor 3	AIC	ΔAIC
+	– **				819.3	0
+	– **			–	819.9	0.6
	– **				820.4	1.1
+	– **		+		821.1	1.8
+	– **	+			821.2	1.9
	– **			–	821.6	2.3
+	– **	+		–	821.9	2.6
+	– **		+	–	821.9	2.6
	– **		+		822.2	2.9

4.2k Rufous Hornbill *Buceros hydrocorax*

Factor 1	Factor 2	AvAlt	AvGirth	Factor 3	AIC	ΔAIC
				–	962.5	0
			+	–	963	0.5
	–			–	963.1	0.6
		+		–	963.2	0.7
–				–	963.6	1.1
	–		+	–	963.7	1.2
			+		964	1.5
–			+	–	964	1.5
	–	+		–	964	1.5
		+	+	–	964	1.5

4.2l Luzon Tarictic *Penelopides manillae*

AvSlope	AvPath	Factor 2	Factor 3	AvAlt	AIC	ΔAIC
– *	–		+	– ***	880.7	0
– *			+	– ***	881.6	0.9
– *	–	+	+	– ***	881.8	1.1
– *	–			– ***	882	1.3
	–		+	– ***	882.3	1.6
– *				– ***	882.8	2.1
– *		+	+	– ***	882.9	2.2
– *	–	+		– ***	883.1	2.4
	–			– ***	883.4	2.7
			+	– ***	883.5	2.8
	–	+	+	– ***	883.5	2.8
– *		+		– ***	884	3.3
				– ***	884.5	3.8
	–	+		– ***	884.6	3.9
		+	+	– ***	884.9	4.2
		+		– ***	885.8	5.1

4.2m Flame-breasted Fruit-dove *Ptilinopus marchei*

AvAlt	AvPath	Factor 3	AveSlope	Factor 1	AIC	ΔAIC
+***			–		235.8	0.0
+***	–			–	236.2	0.4
+***			–	–	236.5	0.7
+***	–		–		236.8	1.0
+***	–		–	–	237.5	1.7
+***		–	–		237.8	2.0
+***	–	–		–	238.0	2.2
+***		–	–	–	238.3	2.5
+***	–	–	–		238.8	3.0
+***	–	–	–	–	239.3	3.5

4.2n Green Imperial-pigeon *Ducula aenea*

AvGirth	AvAlt	CCover	AvPath	AvSlope	AIC	ΔAIC
+	–			–	216.3	0
+				–	216.3	0
+		+		–	216.7	0.4
+	–	+		–	216.8	0.5
+			–	–	217.1	0.8
+	–		–	–	217.2	0.9
				–	217.5	1.2
	–			–	217.9	1.6
		+		–	218	1.7

4.2o Blue-naped Parrot *Tanygnathus lucionensis*

Factor 1	Factor 3	AvGirth	AvSlope	Factor 2	AIC	ΔAIC
				–	82.37	0.00
	–			–	82.55	0.18
–	–			–	83.38	1.01
–				–	83.60	1.23
		+		–	83.70	1.33
	–	+		–	83.80	1.43
			–	–	83.97	1.60
–	–	+		–	84.26	1.89

4.2p Green Racquet-tail *Prioniturus luconensis*

Factor 1	Factor 2	AvAlt	AvSlope	CCover	AIC	ΔAIC
		– *			114.0	0.0
+		– *			114.7	0.7
+		– *		–	114.7	0.7
+	–	– *		–	115.2	1.2
	–	– *			115.4	1.4
		– *	+		115.7	1.7
		– *		–	115.7	1.7
+	–	– *			115.9	1.9
+		– *	+		116.3	2.3

4.2q Blue-crowned Racquet-tail *Prioniturus discurus*

Factor 1	Factor 2	AvAlt	AvPath	CCover	AIC	ΔAIC
–		–	+		57.26	0.00
		–	+*		57.34	0.08
–	–	–	+		57.68	0.42
	–	–	+		57.85	0.59
–		–	+	+	57.98	0.72
–	–	–	+	+	58.57	1.31
–	–	–			58.58	1.32
–		–			58.65	1.39
		–	+	+	59.34	2.08
		–			59.76	2.5

4.2r Luzon Racquet-tail *Prioniturus montanus*

AvPath	AvAlt	Factor 1	Factor 2	Factor 3	AIC	ΔAIC
–	+***	–		–	94.79	0
–	+***			–	95.92	1.13
–	+***	–	+	–	96.77	1.98
–	+***		+	–	97.47	2.68
–	+***				97.81	3.02
	+***	–		–	97.89	3.1
–	+***		+		98.28	3.49
–	+***	–			98.32	3.53
	+***			–	99.06	4.27
–	+***	–	+		99.21	4.42

4.2s Species richness

Factor 2	AvGirth	AvSlope	Factor 1	Factor 3	AIC	ΔAIC
+	+***	_**			1256	0
	+***	_**			1257	1
+	+***	_**	+		1257	1
	+***	_**	+		1258	2
+	+***	_**		+	1258	2
	+***	_**		+	1259	3
	+***	_**	+	+	1259	3
+	+***	_**	+	+	1259	3

4.4.3 Identifying non-linearities in frugivore-habitat associations

From 216 cases of frugivore-habitat associations involving four environmental variables and 18 frugivores, there were 48 linear and 19 quadratic relationships between species and variables (Table 4.4). Only five non-linear relationships were detected (Figure 4.1a-e). In two of the complex cases, the relationship was with tree girth and the terrestrial pigeons Common Emerald Dove and Luzon Bleeding-heart. Green Racquet-tail also showed non-linear relationship with tree girth. The remaining two non-linear relationships were with canopy cover and with Black-chinned Fruit-dove and Green Imperial-pigeon. The analyses using species richness yielded significant correlations with girth. Moreover, the strongest (lowest AIC values) relationships were linear for all the variables considered.

Table 4.3 Summary of habitat association models across frugivore species in Luzon with their corresponding Akaike weights. Figures in bold are significant relationships to variables. IUCN threat status: NT = near threatened, VU = vulnerable. n = number of bird encounters. The symbols represent the shape of the relationship between species presence and the habitat variable + positive linear; – negative linear; ∩ quadratic.

	AvAlt	**AvSlope**	**AvPath**	**AvGirth**	**CCover**	**F1**	**F2**	**F3**
Species with n>50								
White-eared brown-dove *Phapitreron leucotis* (n=630)	**– 1.00**		– 0.30	+ 0.58	**+ 1.00**	**∩ 0.89**		
Amethyst brown-dove *Phapitreron amethystinus* (n=286)		– 0.25	– 0.30	**+ 0.97**	– 0.31	**∩ 0.68**	∩ 0.42	**∩ 0.73**
Cream-bellied fruit-dove *Ptilinopus merrilli* (NT) (n=79)	**+ 0.92**	∩ 0.38		**+ 0.91**		∩ 0.38		∩ 0.38
Yellow-breasted fruit-dove *Ptilinopus occipitalis* (n=157)			+ 0.47	+ 0.49		+ 0.35	**+ 0.92**	∩ 0.34
Black-chinned fruit-dove *Ptilinopus leclancheri* (n=75)	**– 0.98**	∩ 0.50		**+ 0.96**		**∩ 0.82**	∩ 0.36	
Philippine cuckoo-dove *Macropygia tenuirostris* (n=128)	**+ 0.99**	∩ 0.73	– 0.50	+ 0.55				∩ 0.34
Common emerald dove *Chalcophaps indica* (n=119)	– 0.62		– 0.39		+ 0.37	∩ 0.47	– 0.43	
Luzon bleeding-heart *Gallicolumba luzonica* (NT) (n=87)			– 0.34	+ 0.71	+ 0.34	**+ 0.73**		**∩ 0.80**
Guaiabero *Bolbopsittacus lunulatus* (n=243)				+ 0.25	+ 0.30	**+ 0.85**	**∩ 0.90**	+ 0.31
Colasisi *Loriculus philippensis* (n=137)		**– 0.95**		+ 0.27		+ 0.67	∩ 0.28	∩ 0.40
Luzon hornbill *Penelopides manillae* (n-165)	**– 0.99**	**– 0.70**	– 0.62				+ 0.36	∩ 0.53
Rufous hornbill *Buceros hydrocorax* (NT) (n=199)	+ 0.39			+ 0.45		– 0.41	– 0.43	∩ 0.64

Table 4.3 continued

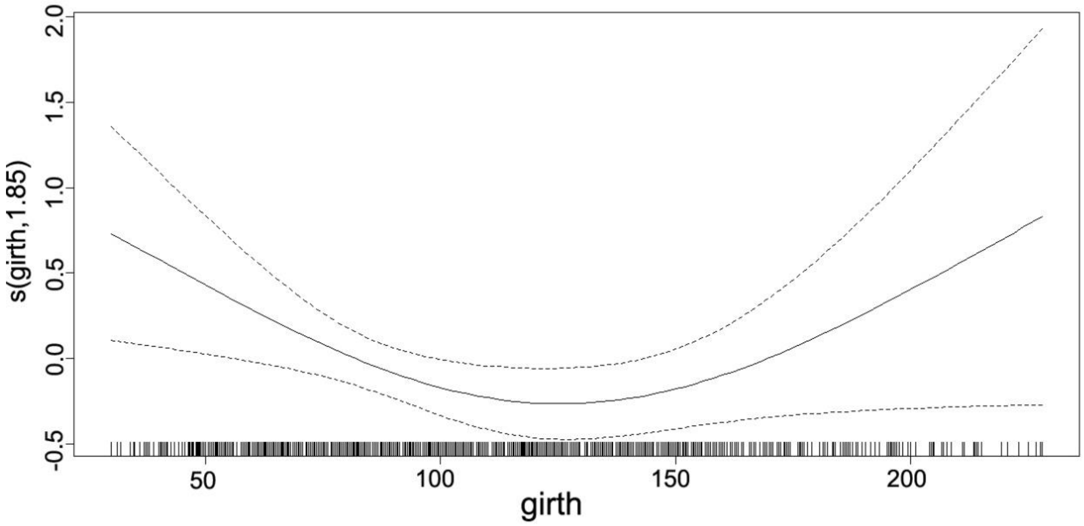
	AvAlt	**AvSlope**	**AvPath**	**AvGirth**	**CCover**	**F1**	**F2**	**F3**
Species with n<50								
Flame-breasted fruit-dove *Ptilinopus marchei* (VU) (n=36)	**+** **1.00**	∩ 0.76	– 0.52			∩ 0.55		∩ 0.28
Green imperial-pigeon *Ducula aenea* (n=30)	– 0.48	– 0.74	– 0.37	+ 0.69	+ 0.42			
Blue-naped parrot *Tanygnathus lucionensis* (VU) (n=11)		∩ 0.31		+ 0.36		– 0.39	∩ 0.77	– 0.51
Green racquet-tail *Prioniturus luconensis* (VU) (n=14)	– 0.95	+ 0.30			– 0.43	+ 0.53	– 0.37	
Blue-crowned racquet-tail *Prioniturus discurus* (n=9)	– 0.77		+ 0.69		– 0.34	– 0.58	– 0.47	
Luzon racquet-tail *Prioniturus montanus* (NT) (n=11)	**+** **1.00**		– 0.81			∩ 0.57	∩ 0.33	∩ 0.76
Species richness		**–** **0.97**		**+** **1.00**		+ 0.39	+ 0.61	+ 0.29

Table 4.4 AIC scores for GAMM model analyses of frugivore-habitat associations. Figures in bold are the best models with the lowest AIC values. Quad = quadratic. K=3 refers to the number of kernels which is three in the GAMM analyses.

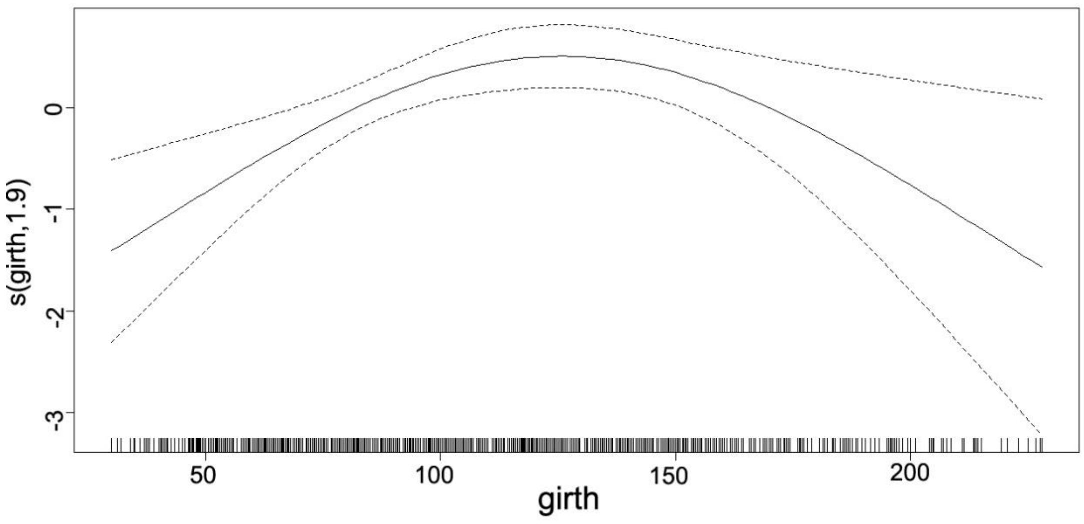
	TREE GIRTH			CANOPY COVER			FACTOR 1			FACTOR 2		
	Linear	Quad	k=3	Linear	Quad	k=3	Linear	Quad	k=3	Linear	Quad	k=3
White-eared brown-dove	**1169.00**	1312.00	1171.00	**1165.00**	1312.00	1167.00	1168.00	**1163.00**	1165.00	**1167.00**	1169.00	1169.00
Amethyst brown-dove	**922.20**	1039.00	924.20	**935.50**	1052.00	937.50	939.70	**937.80**	941.50	939.10	**936.90**	938.70
Cream-bellied fruit-dove	**443.00**	492.50	445.00	**452.20**	500.70	454.20	451.10	**450.30**	452.70	452.20	**452.00**	454.20
Yellow-breasted fruit-dove	**656.50**	767.00	658.50	**659.80**	766.80	661.80	660.80	**660.20**	662.70	**656.10**	661.90	657.80
Black-chinned fruit-dove	**413.00**	476.30	415.00	421.30	476.40	**418.00**	420.30	**415.80**	418.60	420.10	**419.90**	421.40
Philippine cuckoo-dove	**523.50**	676.30	525.50	**524.30**	676.20	526.30	525.70	**525.00**	527.70	525.70	**525.60**	527.70
Common emerald dove	563.30	633.90	**561.70**	**564.10**	635.10	566.00	563.80	**563.40**	565.80	**562.50**	564.00	564.50
Luzon bleeding-heart	504.00	540.90	**497.30**	**505.20**	540.60	507.20	**502.90**	503.20	504.70	505.60	**504.80**	507.60
Guaiabero	**903.80**	1013.00	905.80	**904.50**	1015.00	906.50	**901.50**	902.60	903.40	904.20	**900.70**	905.50
Colasisi	**697.70**	713.60	699.70	**697.30**	713.30	699.30	**694.70**	697.40	696.70	**695.70**	697.40	697.70
Luzon hornbill	**727.90**	757.80	729.90	**734.80**	795.90	736.80	**734.80**	734.80	736.80	**732.80**	734.80	734.80
Rufous hornbill	**821.40**	888.60	823.40	**821.10**	888.60	822.90	**820.10**	823.10	822.10	**823.00**	823.10	825.00
Flame-breasted fruit-dove	**261.70**	296.10	263.70	**262.10**	296.10	263.90	262.00	**260.70**	264.00	**261.00**	262.00	263.00
Green imperial-pigeon	**200.10**	255.00	202.10	202.00	254.80	**200.70**	**202.00**	202.50	204.00	202.50	**202.50**	204.50
Blue-naped parrot	**83.68**	124.00	85.68	**83.67**	123.90	85.67	**83.25**	83.79	85.25	83.96	**80.38**	84.74
Green racquet-tail	114.80	142.60	**113.90**	**114.10**	142.50	116.10	**114.00**	114.60	116.00	**114.40**	114.90	116.40
Blue-crowned racquet-tail	**52.22**	87.50	54.22	**51.96**	86.85	53.10	**46.98**	51.09	48.98	51.05	**47.43**	49.97
Luzon racquet-tail	**105.50**	117.40	107.50	**105.50**	117.00	107.50	105.50	**104.00**	107.40	105.40	**105.00**	107.40
Species richness	**1264.00*****	1278.00***	1266.00***	**1282.00**	1295.00	1284.00	1282.00	**1281.00**	1284.00	**1280.00**	1281.00	1281.00

Figure 4.1 Non-linear bird-habitat relationships detected by the GAMM analyses which show important thresholds in species occurrence as a function of tree girth and canopy cover.

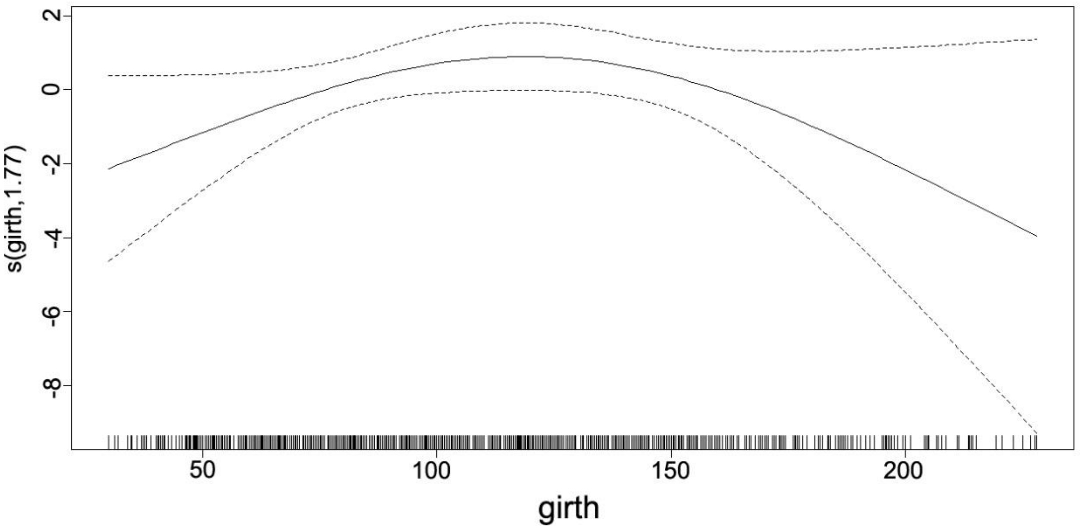
4.1a Increasing presence of Common Emerald Dove *Chalcophaps indica* with increasing tree girth beyond approximately 125 cm.



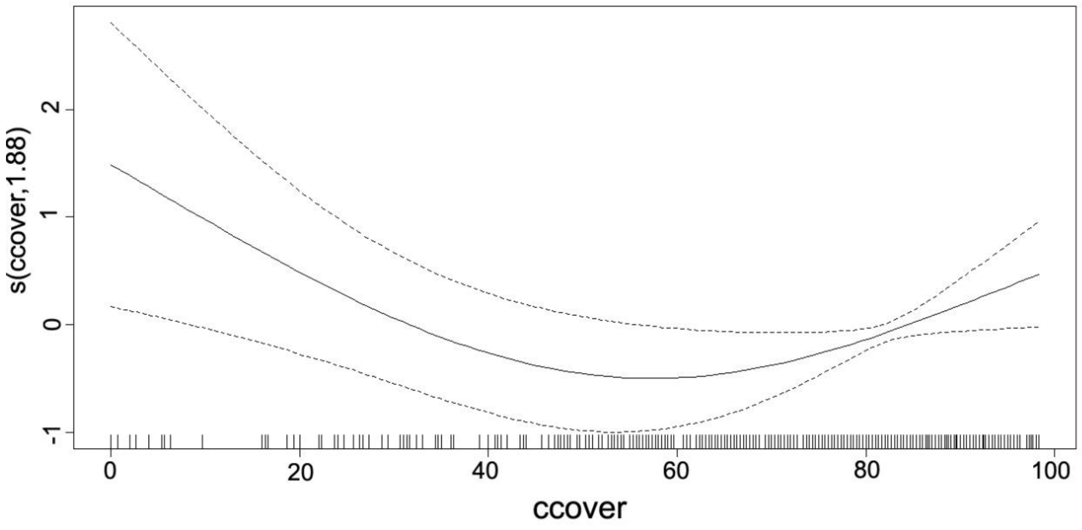
4.1b Decreasing presence of Luzon Bleeding-heart *Gallicolumba luzonica* with increasing tree girth beyond approximately 150 cm.



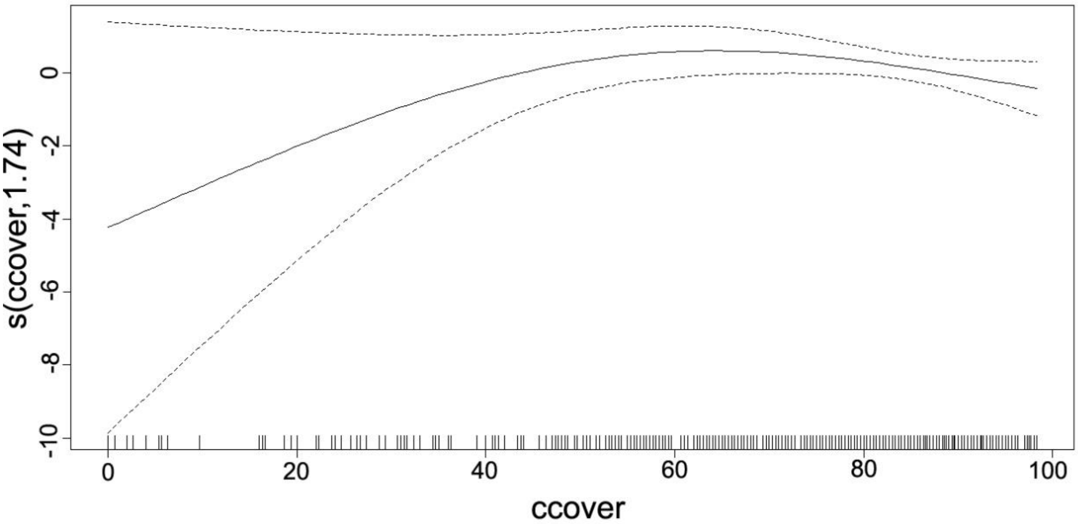
4.1c Decreasing presence of Green Racquet-tail *Prioniturus luconensis* at tree girths beyond approximately 150 cm.



4.1d Increasing presence of Black-chinned Fruit-dove *Ptilinopus leclancheri* with increasing canopy cover beyond approximately 60%.



4.1e Decreasing presence of Green Imperial-pigeon *Ducula aenea* at canopy cover beyond approximately 70%.



4.5 DISCUSSION

Of the habitat variables considered, the main correlates of species richness and presence of most individual species were altitude, slope, tree girths, canopy cover, and Factor 2, a correlate of secondary forest. Two major points emerge from this analysis and will be discussed in turn. First, habitat associations of frugivores proved to be highly individualistic with no two species sharing exactly the same set of habitat correlates or the same response to the correlates. Second, birds appear to respond to a complex of habitat attributes that include geographic, structural and floristic factors. Habitat variables appear to be intimately related and were unlikely to act solely. A study in another island in the Philippines has demonstrated similar linked effects of geography, structure and floristics on bird assemblages (Lee and Marsden, 2008b).

Variation in the response of birds to fine-scale habitat gradients, e.g. vegetation type, may reflect differences in microstructure, especially the foliage characteristics of individual plant species which may affect foraging efficiency and concealment from predators (Cody, 1985). Moreover, certain plant species may provide important resources to birds (Karr and Freemark, 1983). Pioneer plant species, e.g. *Macaranga*, supply frugivores with a bounty of fleshy fruit as opposed to dipterocarp species with inedible pericarp (Corlett and Primack, 2005). Young secondary forest and agroforest sites, which typify Factor 2 habitat, were particularly important ecotones, having not only pioneer plant species but an abundance of figs and human-planted crops that are also potential food sources. Yellow-breasted Fruit-dove and Luzon Hornbill are specialists in this kind of matrix habitat although the former also prefers large trees, which indicates its preference for a more mature secondary forest.

Mature forest offers birds a different complement of resources because of its different habitat structure and vegetation type, often dominated by large dipterocarps with palm trees in the understorey (Corlett and Primack, 2005). A cavity-nesting bird, the 'Near Threatened' Rufous Hornbill, as expected showed preference for trees with large girth, although counterintuitively it was averse to increasing measures of rich lowland forest (Factor 1) and to measures of forest disturbance (Factor 2). It was instead found to prefer high-altitude forest (Factor 3). Species having high Akaike weights for Factor 1 and/or other indicators of good forest, e.g. big tree girth and high canopy cover, include the 'Near Threatened' Cream-bellied Fruit-dove and Luzon Bleeding-heart as well as the relatively common White-eared Brown-dove, Amethyst Brown-dove, Black-chinned Fruit-dove and Green Imperial-pigeon. A weak predictor variable, canopy cover had highest Akaike weight for only one species—White-eared Brown-dove. Frugivores showed an inconsistent response to canopy cover in that three species had a negative relationship with it and five were positive. This is contrary to a study on population trends in Neotropical birds where light penetration was found to be a key variable limiting species occupancy (Patten and Smith-Patten, 2012). It is surprising that species such as the White-eared Brown-dove, common and generally considered to be tolerant of heavily disturbed habitats, were strongly associated with primary forest features. They were certainly observed in secondary forests but had higher abundance in good intact forests (see Table 5.2).

Altitude, known as one of the fundamental drivers of bird distribution (Wiens, 1989), was the most powerful driver of species distribution for Luzon's frugivores. It had the highest Akaike variable weights for ten species. Since altitude was slightly correlated with Factor 3 ($r_s = 0.21$), slope ($r_s = 0.25$) and tree girth ($r_s = 0.10$), many of the species strongly correlated with altitude were also strongly associated with mid-values for Factor 3 and/or slope, i.e. Cream-bellied Fruit-dove, Philippine Cuckoo-dove, Flame-breasted Fruit-dove and Luzon Racquet-tail. Compared to lowland tropical rainforests cloud forests generally have shorter trees, higher stem density, gnarled and twisted trunks and branches, dense and compact crowns, and tough but smaller leaves (Peh *et al.*, 2011). A closer look at vegetation structure and topographic gradients in cloud forests may help elucidate specific factors driving habitat association in high-altitude sites. It is important to note that levels of disturbance in upland sites are much reduced compared to lowland sites, which are more susceptible to logging and agricultural pressures. Similarly, sites with steep slopes may act as refuge from hunting or poaching because of their relative inaccessibility, and they are likely to retain trees that cannot be reached by loggers (Cleary *et al.*, 2005). Upland sites and steep slopes may represent sites where essential resources for birds could be found such as food, shelter, and breeding space. That the 'Vulnerable' Green racquet-tail was the only species positively associated with steep slopes is possibly an indication that this parrot is being pushed to the edge of its known habitat in good lowland forests as has been shown for other species (Hawkins, 1999, Lambert and Collar, 2002). Of the four species averse to steep slopes, three were also averse to wide forest trails and one was correlated with increasing lowland forest quality.

Path width was not a good predictor variable in that it failed to get the highest Akaike weight for any of the species and also had low Akaike weights across all species considered. However, it got the second highest Akaike weight for Blue-crowned Racquet-tail and Luzon Racquet-tail although the relationship was positive for the former and negative for the latter. Blue-crowned Racquet-tail was recorded in just one site in Luzon, which was in a coastal limestone forest that was highly disturbed and planted to coconut trees near the beach. This is not a pattern consistent for the species in its entire range, as it also occurs in very good lowland to submontane forests in Negros (pers. obs.). In contrast, the Luzon Racquet-tail was recorded in mostly intact montane forest with minimal disturbance if any.

Several species including those of conservation concern, i.e. the 'Vulnerable' Flame-breasted Fruit-dove, Blue-naped Parrot and Green Racquet-tail, and the 'Near Threatened' Luzon Racquet-tail (BirdLife International, 2010), had habitat associations that were difficult to model owing to very low encounter rates which resulted to wide variances. It is doubtful whether the habitat association models based on the few sites at which the species were recorded have accurately captured their preference. It is likewise difficult to separate the effects of ecological and life-history traits on rarity although Cofre *et al.* (2007) found evidence that rarity in terms of species distribution was associated with low investment in reproduction, non-migratory status and a degree of habitat specialization. The same authors also found that rarity in terms of abundance was regulated by resource requirements and availability.

The relationships between frugivore presence and habitat features were usually simple linear or quadratic. It was perhaps surprising how few non-linear relationships there were. Overall, 48 from 216 were linear and 19 were quadratic – only five were more complex. Even the complex relationships appear closer to quadratic when graphed

(Figures 4.1a-e). Such complex relationships need to be identified when examining the response of birds to environmental variables as simply considering linear relationships can be misleading conservation-wise (Meents *et al.*, 1983). These simple relationships suggest that management prescriptions can be simply formulated. It also means that improvement to habitat quality all along the forest quality gradient from very degraded to intact forest is expected to improve the habitat for frugivores (Naidoo, 2004).

Six of the 18 frugivore species considered including the 'Near Threatened' Cream-bellied Fruit-dove and Luzon Bleeding-heart were strongly dependent on good forest. The rest required some measure of good forest but were tolerant of disturbance to a degree. This reinforces the importance of habitat heterogeneity for maintaining bird diversity within reserves as no single habitat can provide the needs of all species. Nevertheless, forest quality in Luzon especially within protected areas by and large is decreasing (Verburg *et al.*, 2006). Very good forests are being degraded through illegal logging while very poor forest is being wiped out by fire and total clearance for agriculture and development. All these have and will continue to affect frugivores. Although a few 'non-forest' or large open country frugivores, e.g. bulbuls and orioles, occur in Luzon, they will never be able to replace forest frugivores in their role of forest regeneration.

Chapter 5

DENSITY ESTIMATION IN LUZON'S FRUGIVORES: CORRECTING FOR EFFECTS OF HABITAT, AND NON-RANDOM PLACEMENT OF SAMPLING ALONG PATHS

5.1 ABSTRACT

Precise and accurate estimates of wildlife population density and sizes are essential to provide evidence for effective wildlife management and conservation programmes. Line transect distance sampling is a robust method in that variability in detectability due to distance from the transect line and covariates is taken into account in species density estimates. Many conservation studies cannot, by necessity, be based on random transect placement, instead use transects along existing trails. This study estimates the bias due to this in estimates of species densities, encounter rates, effective strip widths and overall detection function along three path categories—random paths (specially-cut transects), hunter trails (path width <100cm) and access roads (path width >100cm). Differences in floristic and vegetation structural features as well as human disturbance in the form of hunting were responsible for the difference in species density estimates across path types. Path types were similar in measures of altitude and the presence of fig, bamboo and pioneer trees and differed especially in terms of tree girths, slope, canopy cover, and presence of crops, dipterocarp trees and attributes of secondary forest. Hunter trails yielded lowest densities and encounter rates for nine of 12 species and lowest effective strip width for seven of 12 species. Highest densities and encounter rates were along random paths for seven of 12 species. Differences in density across trail types were driven by differences in encounter rates rather than differences in detectability. Average encounter rate across path types is 206% compared to 143% for effective strip width.

Correction of density estimates from a survey with biased transect placement produced higher values of up to 287% difference compared to raw estimates. The average difference between raw and corrected estimates is 190% (118-287%). In fragmented forests where random placement of transects is not always possible, this method of correction will allow species density estimates from sampling along hunter trails and access roads to be adjusted.

5.2 INTRODUCTION

The quantification of wildlife populations is an essential component of effective species management and conservation programmes, and is particularly critical within reserves supporting populations of threatened species (Thompson, 2002, Newton *et al.*, 2004). Sampling methods are the means employed to quantify most wildlife populations since censuses or total counts are usually not feasible and prohibitively expensive (Marques and Buckland, 2003). A key assumption of any such sampling is that an estimate of a sample or fraction of the population accurately reflects the true population size of the survey region.

A widely used sampling method in estimating wildlife populations and birds in particular is line transect distance sampling (LTDS) (Buckland *et al.*, 2001). When assumptions for the implementation of LTDS are met, it gives a precise and accurate estimate of species density or number of birds per unit of area. The assumptions are (1) transects are randomly placed in the survey area, (2) all animals or clusters of animals along the transect are detected, (3) animals are detected at their initial location and prior to any responsive movement to the observer, and (4) distances are accurately measured or estimated with minimal errors (Buckland *et al.*, 1993). The method is robust in that it takes into consideration changes in detectability with distance away from the transect line (Buckland *et al.*, 2001). Successive work has incorporated the effects of covariates including habitat, observer, bird behaviour, weather conditions, etc. on detectability (Marques *et al.*, 2007, Marques and Buckland, 2003).

Meeting the assumption of random placement of transects is not always possible in many different habitats e.g. tropical forests because of the density of vegetation and steep slopes along ridges, wetland because of impassable bogs or quicksand, and farmland because of restrictions both physical (fences) and ethical (i.e. trampling of crops). Completely random placement of samples is difficult in the tropics unless the survey team has a lot of manpower or if there is a grid of trails specially cut (e.g. Johns 1996). An alternative used by Jones *et al.* (2001) was to survey along existing trails but to place point counts 20-50 m off the trail within the forest. Lee (2005) found serious effects of logging paths on the densities of birds on Mindoro, Philippines, but his survey suffered from the problem of small number of replicates. This is clearly an important issue, in respect of safety of fieldworkers and reliability of results, however, little research has been undertaken on the effects of surveying along non-random features (Marques *et al.*, 2010, Marques *et al.*, 2012), especially in the tropics (Hilario *et al.*, 2012). Marques *et al.* (2012) has found distance surveys that assume uniform species distribution from landscape features such as roads produced a -20% bias in density estimates of Eastern Grey Kangaroo *Macropus giganteus*. There are exceptions as some species such as the Wild Turkey *Meleagris gallopavo* are randomly distributed relative to non-random land features such as roads so road surveys yield unbiased results (Erxleben *et al.*, 2011).

In this study, I have tested the degree of bias that LTDS on non-random transects has on estimates of density, encounter rate and effective strip width. LTDS was used to estimate abundance of avian frugivores, a group deemed important for their role in seed dispersal and forest regeneration. Sampling was conducted along line transects classified according to three path categories based on measures of increasing path width and known levels of hunting disturbance: random paths, hunting trails and access roads. In order to measure the bias resulting from conducting sampling along non-random transects, I compared species densities, encounter rates (birds encountered per unit effort), effective strip width (ESW) (the distance from the line at which as many animal clusters are detected beyond the given distance as are missed within the given distance from the line) and detection function (probability that an animal is detected as a function of distance from the line) across path categories. This bias can be corrected in completed surveys as I have demonstrated in density data from surveys in the Sierra Madre in 2010. Knowledge of this bias will allow extrapolation of results to a wider area and will benefit the design and conduct of future surveys.

5.3 METHODS

5.3.1 Field methods: bird counts and habitat measures

Bird and habitat data were collected from December 2011 to February 2012 at Subic Bay Forest Reserve and Bataan National Park in western Luzon (Fig. 5.1). Sixteen frugivorous bird species were sampled using LTDS methods described in Section 2.3.3. Transects were categorized according to their measures of path width as random paths (paths specially cut in the forest), hunter trails (existing paths <100cm in width) and access roads (existing paths >100cm in width) (Fig. 5.2). Random paths were specially-cut transects that didn't follow any obvious land feature such as ridges, flat land, rivers or other bodies of water. Hunter trails were narrow paths regularly used by hunters and farmers along forested edges of farms or logging roads. Hunter activity was mostly confined to the use of snares to capture prey but in some areas airguns and dogs are used to track and retrieve prey. Local people also use these hunter trails to collect non-timber forest products such as rattan, honey, seedlings, snails, frogs, forest fruits, etc. Wider forest paths showing evidence of cattle or vehicle traffic were categorized as access roads.

Examples of access roads include 'buffalo-assisted logging' roads and farm-to-market roads.

Figure 5.1 Map of transects across the study area in Subic Bay Forest Reserve and Bataan National Park. Yellow lines are transects along random paths, pink lines are along hunter trails and red lines are along access roads.

Figure 5.2 Examples of the three path types in Luzon, Philippines. A = random or specially-cut path, B = narrow hunter trail, C = cattle and/or vehicle access road

Habitat measures were taken for each 400m transect segment in 10x20m habitat plots following methods detailed in Section 4.3.1. Habitat variables included structural and floristic factors as well as a Principal Components Analysis (PCA) composite axis of floristic factors that characterize the major forest types in the study area, i.e. primary forest, secondary forest and regenerating forest (see Section 4.3.2). Structural factors include altitude, tree girth, slope, path width and canopy cover. Floristic factors were occurrence records of plant types and habitat features known to be important for frugivores, such as planted crop, palm, fig, rattan, dipterocarp, epiphyte, bamboo, pioneer trees, liana and standing dead trees. Percentile values of habitat variables were obtained after which a pair-wise comparison of habitat features across the three path categories was carried out using the Mann-Whitney-Wilcoxon Test.

5.3.2 Density estimation across path types

The MCDS (Multiple Covariates Distance Sampling) engine of DISTANCE 6.0 release 2 software (Thomas *et al.*, 2010) was used to estimate species-specific densities (individuals km^{-2}) in the different path categories. Species with less than 30 observations/encounters were excluded from the distance analysis but encounter rates were computed instead. Bird records were entered as clusters (number of birds in a flock) with distances divided (or grouped) into intervals whenever rounding of distances to favoured values (e.g., nearest 10 or 15 m) or bird movement prior to detection was evident, following Buckland *et al.* (2001) and Thomas *et al.* (2010). Outlying records at large distances away from the transect line were removed since they contribute little to the calculated density estimate and hinder model fitting (Buckland *et al.*, 2001, Thomas *et al.*, 2010). I determined the cut-off point for the analyses by fitting a preliminary model and removing observations with less than 0.15 detection probability (Buckland *et al.*, 2001). Models were built using the half-normal and hazard rate key functions each in combination with covariates thought to influence the probability of detection, namely sampling month, and average canopy cover and tree girth per transect. Several exploratory analyses using the multivariate models with different truncation values and distance intervals were run with the optimal detection function for each species selected based on minimisation of Akaike's Information Criterion (AIC) values and coefficient of variation of the density estimate. With competing models or where model choice was uncertain, a comparison of goodness-of-fit measures between models was made (Marques *et al.*, 2007). A nonparametric bootstrap was used to estimate variance by sampling with replacement using transects as resampling units (Buckland *et al.*, 2001).

5.3.3 Density correction of first field season data

Species density estimates in section 5.2.2 were used to compute the percentage difference in density across path types (Table 5.3). This then allowed for a correction factor to be used in adjusting species densities estimated from the first field season data (those presented in Chapter 2) to correct for the bias in non-random transect placement. As a demonstration, I considered two sites with high numbers of bird records for the analysis: Aurora and the combined Isabela and Cagayan sites. Transects in each site were parsed into two equally-sized groups of either closed or open canopy forest using the median measure of average canopy cover per transect. These were 71% in Isabela and Cagayan, and 75% in Aurora. Transects with average canopy cover values below the median were placed in the open canopy category and transects with values above the median in the closed canopy category. Only six species had enough bird records in the aforementioned sites for density estimates to be used in this analysis. There were so few records of Colasisi *Loriculus philippensis* in Aurora and of Luzon Hornbill *Penelopides manillae* in Isabela and Cagayan that these species were excluded from the analyses for these sites.

5.4 RESULTS

5.4.1 Differences in habitat across path types

Table 5.1 shows the comparison of environmental correlates across different path types in the survey using the Mann-Whitney-Wilcoxon Test. Two habitat measures, path width and presence of crops, were significantly different in all three path types. On the other hand, altitude and the presence of fig, bamboo and pioneer trees were not significantly different across path types.

Random paths had higher values of most 'habitat variables' compared to hunter trails and access roads (Table 5.1). Random paths were mainly characterized by minimal evidence of human alteration such as low occurrence of planted crops, a thick and dark understorey of dense liana and rattan, and an overstorey of large dipterocarp trees. Hunter trails were not significantly different from random paths except for significantly higher measures of path width and presence of crops and lesser density of rattan, liana and dipterocarp trees. Compared to access roads, hunter trails had significantly larger trees, higher values for the floristic composite representing primary forest and more palms; and significantly smaller paths and lesser occurrence of crops. Access roads were characterized by smaller trees, gentler slope, open canopy, and higher occurrence of crops and the floristic composite of secondary forests (Table 5.1).

5.4.2 Densities, encounter rates, detectability and detection functions across path types

Average difference in encounter rates for common species was 200% while average difference in ESW was just 110%. Although not marked for less common species, the average differences were still higher for encounter rates at 211% compared to 180% for ESW. Across species average difference in encounter rates was 206% and 143% for effective strip width.

Table 5.1 Medians and upper/lower percentiles of environmental features across different path types and results of Mann-Whitney-Wilcoxon tests; * p < 0.05; ** p < 0.005

	Random paths	Small hunter/farmer trails	Access roads	Test
Altitude	340 (193-614)	381 (213-647)	267 (200-458)	1<2; 1>3; 2>3
Tree girth	111 (93.5-127)	106 (89.8-124)	85.3 (68.3-120)	1>2; **1>3*; 2>3***
Slope	13.5 (10.0-19.3)	10.9 (8.80-15.8)	10.2 (6.86-13.9)	1>2; **1>3***; 2>3
Path width	0.00 (0.00-4.36)	43.3 (36.1-52.7)	91.2 (65.2-118)	**1<2**; 1<3**; 2<3****
Canopy cover	86.8 (82.4-90.6)	85.4 (79.9-88.6)	81.9 (54.2-89.6)	1>2; **1>3***; 2>3
Primary forest	0.38 (0.24-0.62)	0.33 (0.24-0.56)	0.21 (0.00-0.50)	1>2; **1>3*; 2>3***
Secondary forest	0.30 (0.20-0.41)	0.40 (0.19-0.53)	0.57 (0.29-0.83)	1<2; **1<3**; 2<3***
Regenerating forest	0.23 (0.15-0.33)	0.24 (0.17-0.29)	0.15 (0.07-0.27)	1<2; 1>3; **2>3***
Crop	0.00 (0.00-0.00)	0.00 (0.00-0.10)	0.07 (0.00-0.20)	**1<2*; 1<3**; 2<3***
Palm	0.00 (0.00-0.20)	0.00 (0.00-0.12)	0.00 (0.00-0.00)	1>2; **1>3*; 2>3***
Fig	0.30 (0.22-0.55)	0.33 (0.17-0.42)	0.18 (0.12-0.41)	1<2; 1>3; 2>3
Rattan	0.58 (0.50-1.00)	0.42 (0.37-0.62)	0.37 (0.12-0.54)	**1>2**; 1>3**;** 2>3
Dipterocarp	0.50 (0.30-0.79)	0.30 (0.14-0.49)	0.20 (0.06-0.41)	**1>2**; 1>3****; 2>3
Bamboo	0.00 (0.00-0.18)	0.00 (0.00-0.12)	0.00 (0.00-0.10)	1>2; 1>3; 2>3
Pioneer trees	0.20 (0.01-0.38)	0.17 (0.00-0.29)	0.15 (0.05-0.29)	1>2; 1>3; 2>3
Standing dead tree	0.21 (0.02-0.40)	0.17 (0.01-0.25)	0.03 (0.00-0.20)	1>2; **1>3***; 2>3
Liana	0.60 (0.45-1.00)	0.50 (0.33-0.55)	0.42 (0.26-0.60)	**1>2*; 1>3***; 2>3

Four best models for estimating detection probability were selected by AIC across all species considered: (1) month, (2) tree girth, (3) no covariate, and (4) a combination of month, tree girth and canopy cover. AIC chose a different model for each path type within each species except for the Amethyst Brown-dove, Luzon Hornbill and Green Imperial-pigeon, each of which had the combination of all three covariates as best model for two path types.

Species densities were lowest along hunter trails in five of six common species and highest along random paths in four species (Table 5.2). The Guaiabero was the only common species with highest density along access roads. Among less common species (those with fewer than 30 records in a path category), four of six had lowest densities along access roads while the opposite was true for the Common Emerald Dove and Green Imperial-pigeon, with both having highest densities on access roads. All the common species were at least 124% more abundant or 24% higher in random paths compared to hunter trails with the highest being more than 200% or twice as high in both brown-doves (Table 5.3). The Amethyst Brown-dove was also 261% more abundant on random paths compared to access roads. The Yellow-breasted Fruit-dove had 430% and 263% higher density in random paths and hunter trails respectively compared to access roads.

Table 5.2 Density estimates (D), encounter rates (ER), number of observations (n), effective strip width (ESW), and detection functions for species in different path type. Species are arranged according to the number of observations with the most common species first. D_b are bootstrapped estimates of density. Data were not truncated (TR) in species with records fewer than 12 in a particular path type.

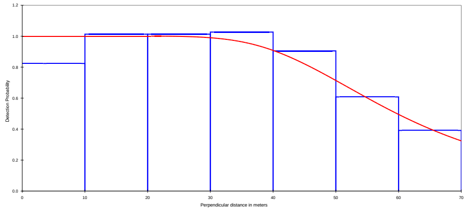
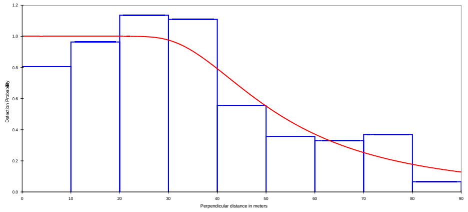
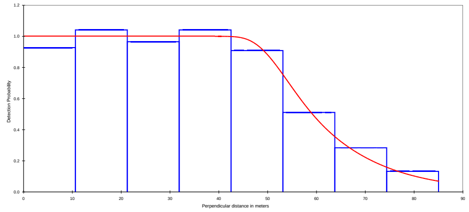
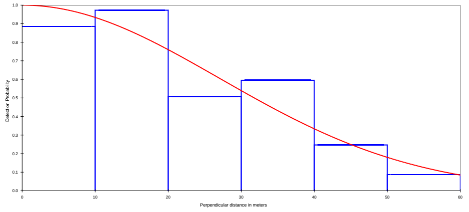
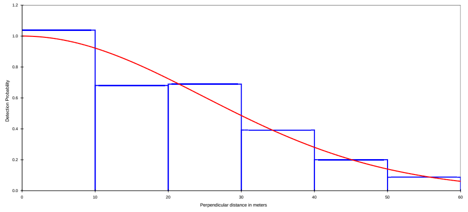
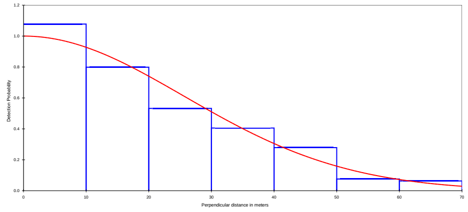
	Random paths	Hunter/farmer trails	Access roads
White-eared Brown-dove *Phapitreron leucotis*	D_b = 37.5 ± 0.14; 27.6-47.9 ER = 4.16 ± 0.17 n = 428 ESW = 57.8 ± 0.02 Best model = Canopy Cover; TR = 70m 	D_b = 17.2 ± 0.20; 10.8-24.2 ER = 1.83 ± 0.23 n = 431 ESW = 56.8 ± 0.05 Best model = no covariate; TR = 90m 	D_b = 28.4 ± 0.18; 19.5-38.9 ER = 3.27 ± 0.16 n = 307 ESW = 61.8 ± 0.03 Best model = Month; TR = 85m 
Guaiabero *Bolbopsittacus lunulatus*	D_b = 41.4 ± 0.19; 28.1-56.8 ER = 2.21 ± 0.11 n = 227 ESW = 33.0 ± 0.06 Best model = no covariate; TR = 60m 	D_b = 31.3 ± 0.17; 20.9-41.7 ER = 1.51 ± 0.16 n = 354 ESW = 30.9 ± 0.04 Best model = Tree Girth; TR = 60m 	D_b = 52.2 ± 0.12; 41.8-63.5 ER = 2.71 ± 0.11 n = 255 ESW = 32.3 ± 0.05 Best model = Canopy Cover; TR = 70m 

Table 5.2 continued

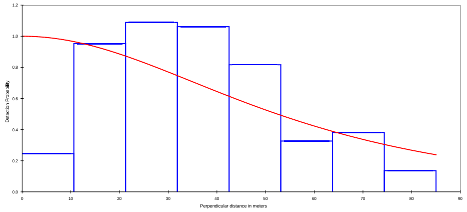
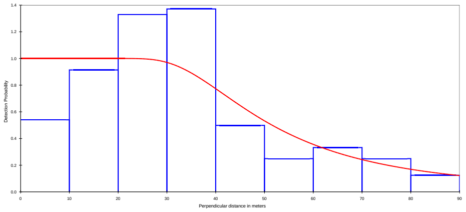
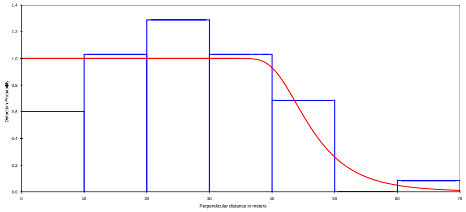
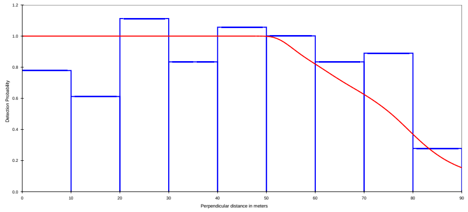
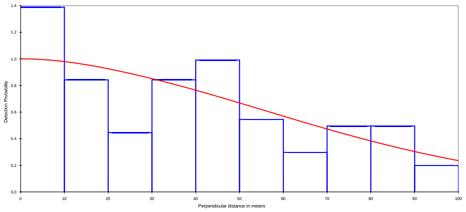
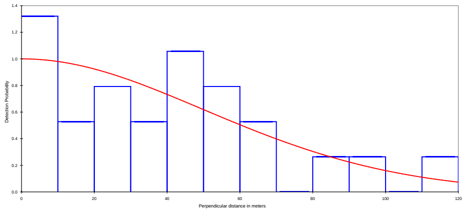
	Random paths	Hunter/farmer trails	Access roads
Amethyst Brown-dove *Phapitreron amethystinus*	D_b = 17.1 ± 0.25; 10.9-24.0 ER = 1.79 ± 0.24 n = 184 ESW = 53.2 ± 0.05 Best model = Month + Canopy Cover + Tree Girth; TR = 85m 	D_b = 5.31 ± 0.34; 2.03-9.81 ER = 0.57 ± 0.31 n = 135 ESW = 56.1 ± 0.05 Best model = Month + Canopy Cover; TR = 90m 	D_b = 6.58 ± 0.32; 2.85-11.0 ER = 0.59 ± 0.33 n = 55 ESW = 47.3 ± 0.06 Best model = no covariate; TR = 70m 
Yellow-breasted Fruit-dove *Ptilinopus occipitalis*	D_b = 8.98 ± 0.26; 4.98-14.0 ER = 1.29 ± 0.23 n = 133 ESW = 74.0 ± 0.04 Best model = Canopy Cover + Tree Girth; TR = 90m 	D_b = 5.42 ± 0.47; 1.68-11.6 ER = 0.56 ± 0.39 n = 132 ESW = 65.4 ± 0.06 Best model = Canopy Cover; TR = 100m 	D_b = 2.58 ± 0.34; 1.16-4.01 ER = 0.26 ± 0.46 n = 24 ESW = 63.4 ± 0.19 Best model = Month; TR = 120m 

Table 5.2 continued

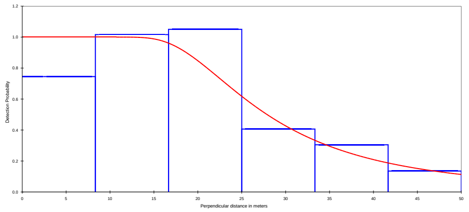
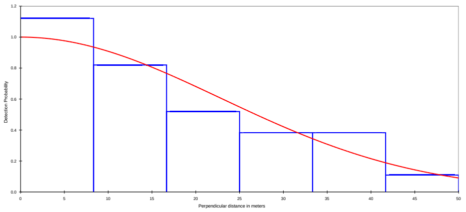
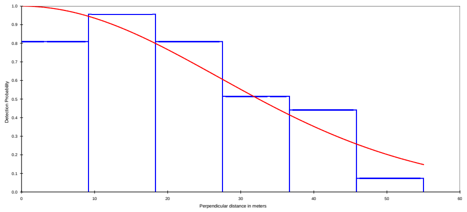
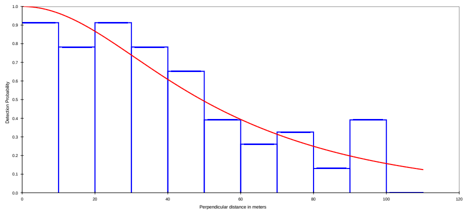
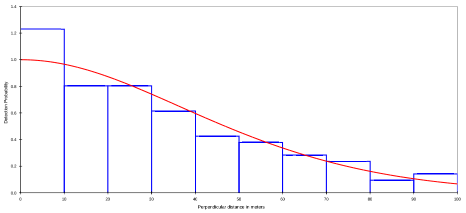
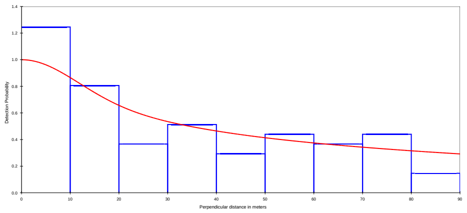
	Random paths	Hunter/farmer trails	Access roads
Colasisi *Loriculus philippensis*	D_b = 19.2 ± 0.21; 12.7-24.5 ER = 1.05 ± 0.21 n = 108 ESW = 30.5 ± 0.06 Best model = Tree Girth; TR = 50m 	D_b = 13.3 ± 0.30; 7.08-22.6 ER = 0.52 ± 0.22 n = 122 ESW = 27.8 ± 0.08 Best model = no covariate; TR = 50m 	D_b = 14.3 ± 0.36; 6.44-24.9 ER = 0.52 ± 0.24 n = 49 ESW = 33.0 ± 0.10 Best model = Month; TR = 55m 
Luzon Hornbill *Penelopides manillae*	D_b = 9.66 ± 0.28; 7.21-14.2 ER = 0.83 ± 0.18 n = 85 ESW = 55.4 ± 0.09 Best model = Month + Canopy Cover + Tree Girth; TR = 110m 	D_b = 8.00 ± 0.23; 4.99-12.1 ER = 0.45 ± 0.17 n = 106 ESW = 50.1 ± 0.07 Best model = Tree Girth; TR = 100m 	D_b = 12.6 ± 0.43; 7.81-17.5 ER = 0.67 ± 0.16 n = 63 ESW = 46.2 ± 0.16 Best model = Month + Canopy Cover + Tree Girth; TR = 90m 

Table 5.2 continued

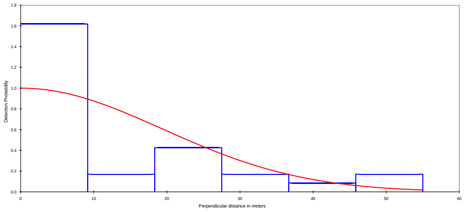
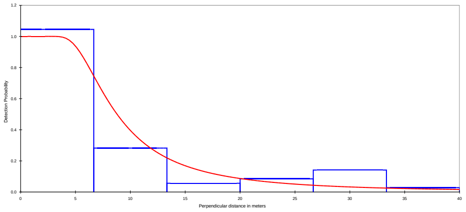
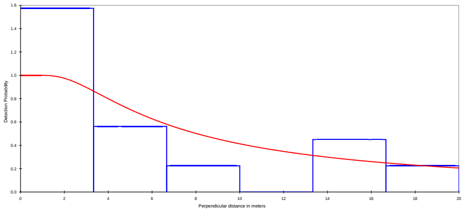
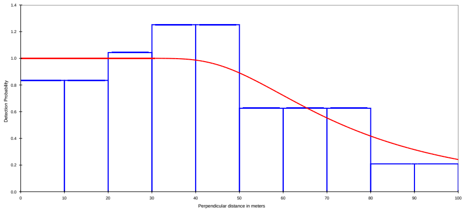
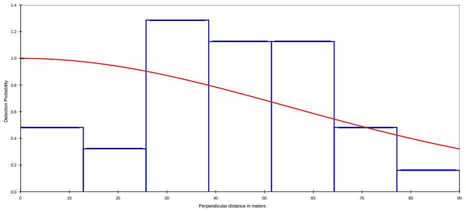
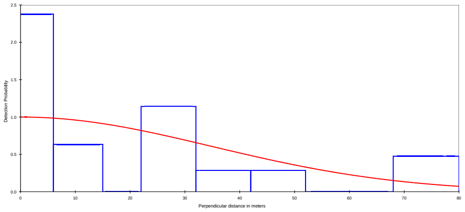
	Random paths	Hunter/farmer trails	Access roads
Common Emerald Dove *Chalcophaps indica*	D = 6.72 ± 0.29; 3.76-12.0 ER = 0.30 ± 0.26 n = 31 ESW = 24.2 ± 0.13 Best model = Month + Canopy Cover; TR = 55m 	D = 12.5 ± 0.34; 6.50-23.9 ER = 0.25 ± 0.28 n = 58 ESW = 10.9 ± 0.19 Best model = Tree Girth; TR = 40m 	D = 14.2 ± 0.29; 8.02-25.1 ER = 0.29 ± 0.23 n = 27 ESW = 10.1 ± 0.17 Best model = Month; TR = 20m 
Green Imperial-pigeon *Ducula aenea*	D = 5.75 ± 0.44; 2.44-13.5 ER = 0.35 ± 0.41 n = 36 ESW = 75.1 ± 0.08 Best model = Month; TR = 100m 	D = 1.54 ± 0.48; 0.62-3.79 ER = 0.13 ± 0.44 n = 31 ESW = 64.1 ± 0.15 Best model = Month + Canopy Cover + Tree Girth; TR = 90m 	D = 8.96 ± 0.57; 3.08-26.1 ER = 0.16 ± 0.47 n = 15 ESW = 42.8 ± 0.18 Best model = Month + Canopy Cover + Tree Girth; TR = 80m 

Table 5.2 continued

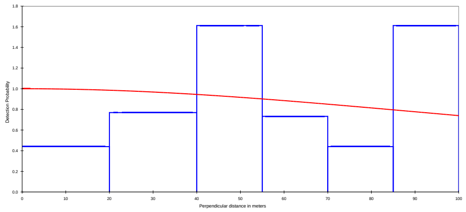
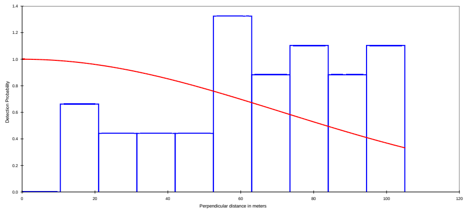
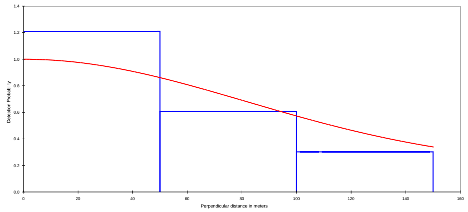
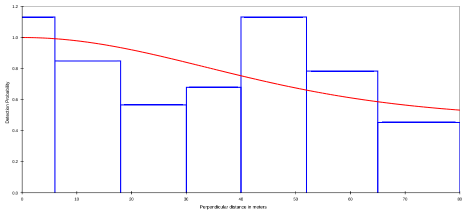
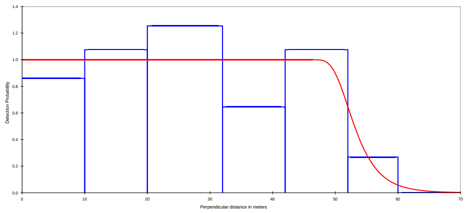
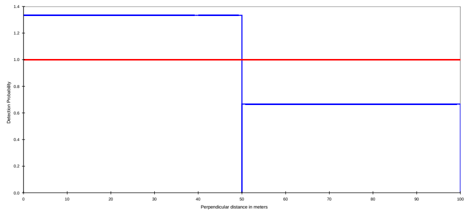
	Random paths	Hunter/farmer trails	Access roads
Philippine Cuckoo-dove *Macropygia tenuirostris*	D = 2.47 ± 0.42; 1.10-5.53 ER = 0.40 ± 0.32 n = 41 ESW = 90.1 ± 0.27 Best model = Tree Girth; TR = 100m 	D = 1.04 ± 0.39; 0.49-2.21 ER = 0.14 ± 0.38 n = 33 ESW = 76.5 ± 0.09 Best model = Month; TR = 105m 	D = 0.49 ± 0.64; 0.15-1.61 ER = 0.07 ± 0.58 n = 7 ESW = 106 ± 0.23 Best model = Month 
Green Racquet-tail *Prioniturus luconensis*	D = 3.15 ± 0.52; 1.18-8.43 ER = 0.18 ± 0.44 n = 18 ESW = 61.1 ± 0.20 Best model = Month + Tree Girth; TR = 80m 	D = 1.41 ± 0.40 ER = 0.11 ± 0.38 n = 25 ESW = 53.7 ± 0.07 Best model = no covariate; TR = 70m 	D = 0.43 ± 0.83; 0.10-1.87 ER = 0.06 ± 0.72 n = 6 ESW = 100 ± 0.38 Best model = Month 

Table 5.2 continued

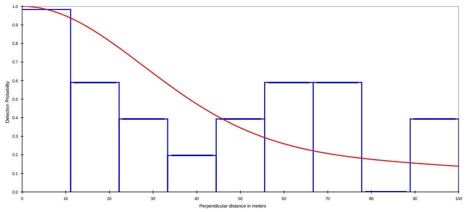
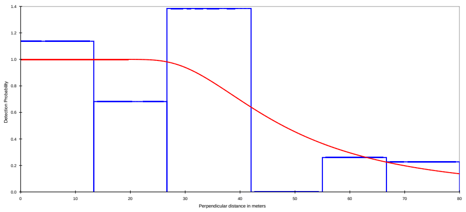
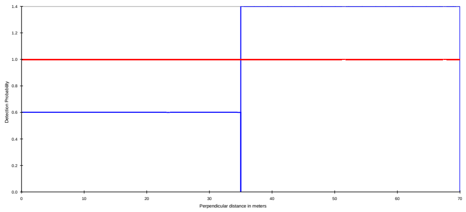
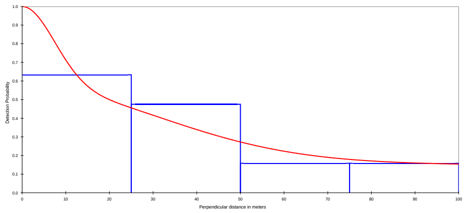
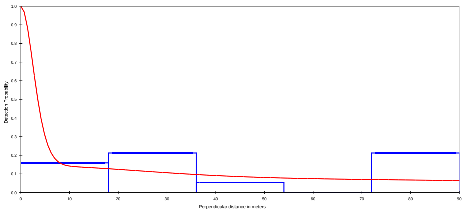
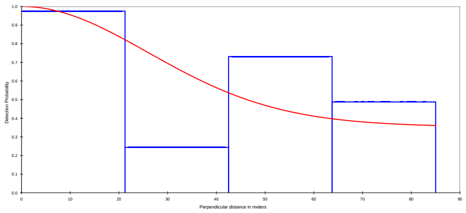
	Random paths	Hunter/farmer trails	Access roads
Pompadour Green-pigeon *Treron axillaris*	D = 2.79 ± 1.01; 0.50-15.52 ER = 0.20 ± 0.44 n = 21 ESW = 45.9 ± 0.90 Best model = Month + Tree Girth; TR = 100m 	D = 2.02 ± 0.38; 0.97-4.23 ER = 0.07 ± 0.30 n = 17 ESW = 51.5 ± 0.14 Best model = Tree Girth; TR = 80m 	D = 1.90 ± 0.60; 0.61-5.90 ER = 0.11 ± 0.34 n = 10 ESW = 70.0 ± 0.31 Best model = no covariate 
Black-chinned Fruit-dove *Ptilinopus leclancheri*	D = 1.23 ± 2.23; 0.05-30.4 ER = 0.09 ± 0.46 n = 9 ESW = 35.6 ± 2.19 Best model = Canopy Cover + Tree Girth 	D = 2.08 ± 0.78; 0.49-8.82 ER = 0.05 ± 0.35 n = 12 ESW = 11.5 ± 21.20 Best model = Tree Girth 	D = 1.16 ± 0.53; 0.42-3.20 ER = 0.11 ± 0.40 n = 10 ESW = 51.8 ± 0.33 Best model = Tree Girth 

Table 5.2 continued

	Random paths	Hunter/farmer trails	Access roads
Rufous Hornbill *Buceros hydrocorax*	ER = 0.12 ± 0.28 n = 12	ER = 0.05 ± 0.35 n = 11	ER = 0.05 ± 0.49 n = 5
Luzon Bleeding-heart *Gallicolumba luzonica*	ER = 0.02 ± 0.68 n = 2	ER = 0.05 ± 0.40 n = 12	ER = 0 n = 0
Blue-naped Parrot *Tanygnathus lucionensis*	ER = 0.06 ± 0.73 n = 6	ER = 0.01 ± 1.00 n = 2	ER = 0.03 ± 0.98 n = 3

Table 5.3 Percentage difference in density estimates, encounter rates and effective strip width between path types 1 (random paths), 2 (hunter trails) and 3 (access roads). More than 200% percentage differences (i.e. one is greater than twice the other) are in bold. The position of the plus sign indicates in which of the path types estimated density (D), encounter rate (ER) or effective strip width (ESW) was higher.

SPECIES	**Density**			**Encounter Rate**			**Effective Strip Width**		
	1&2	**1&3**	**2&3**	**1&2**	**1&3**	**2&3**	**1&2**	**1&3**	**2&3**
Species with total n>250									
White-eared Brown-dove	**+214**	+133	161+	**+227**	+127	179+	+102	107+	109+
Guaiabero	+140	117+	163+	+146	123+	179+	+107	+102	105+
Amethyst Brown-dove	**+292**	**+261**	112+	**+314**	**+303**	104+	+105	+112	+108
Yellow-breasted Fruit-dove	+163	**+430**	**+263**	**+230**	**+496**	**+215**	+126	+122	103+
Colasisi	+175	+157	112+	**+202**	**+202**	100	+110	108+	119+
Luzon Hornbill	+124	104+	129+	+184	+124	149+	+111	+120	+108
Species with total n<120									
Common Emerald Dove	186+	211+	114+	+120	+103	116+	+222	+240	+108
Green Imperial-pigeon	**+373**	156+	**582+**	**+269**	**+219**	123+	+117	+175	+150
Philippine Cuckoo-dove	**+238**	**+504**	**+212**	**+286**	**+571**	**+200**	+118	118+	139+
Green Racquet-tail	**+223**	**+733**	**+328**	+164	**+300**	+183	+114	164+	186+
Pompadour Green-pigeon	+138	+147	+106	**+286**	+182	157+	112+	153+	136+
Black-chinned Fruit-dove	169+	+106	+179	+180	122+	**220+**	**+310**	146+	**450+**

The same five common species with lowest densities along hunter trails also had lowest encounter rates with three of those having lowest effective strip width as well. All the common species had highest encounter rates along random paths except again for the Guaiabero, which was highest on access roads. Likewise for effective strip width, four common and two less common species had highest values along random paths. The Pompadour Green-pigeon was the lone species with lowest effective strip width on random trails. Four of six less common species had encounter rates lowest along hunter trails while three of six less common species had lowest effective strip width. Encounter rates for common species were 146-314% lower along hunter trails compared to random paths and 120-286% lower for less common species. Average percentage difference in effective strip width was low at 110% among common species and 180% for less common species. In the Common Emerald Dove the effective strip width was considerably greater (>200%) for random paths compared to hunter trails and access roads. A large drop in effective strip width along hunter trails in the Black-chinned Fruit-dove generated a 310-450% difference compared to random paths and access roads.

5.4.3 Correction factors for first field season's density data

Corrected density estimates for all species were higher compared to raw estimates (Table 5.4). The Amethyst Brown-dove had the highest percentage difference at 275-288% while Luzon Hornbill had the lowest at 118-120%. The average corrected density estimates in Aurora was higher at closed canopy sites than open canopy sites with 35.0 km^{-2} compared to 25.8 km^{-2}. Conversely, average corrected density estimates at closed canopy sites in Isabela and Cagayan were lower at 26.7 km^{-2} compared to 37.7 km^{-2} in open canopy sites.

Table 5.4 Raw (not accounting for path types) and corrected density estimates (individuals km^{-2} ± CV) for selected frugivores from Aurora and combined Isabela and Cagayan sites from data gathered during the first field season on 2010.

		Aurora		Isabela and Cagayan	
		Closed	Open	Closed	Open
		10/113/9	0/67/18	8/88/9	0/85/15
White-eared Brown-dove	Raw	41.4 ± 13.2	33.4 ± 21.5	21.4 ± 22.1	35.9 ± 20.7
	Corrected	82.7 ± 13.2	65.8 ± 21.5	42.5 ± 22.1	72.5 ± 20.7
Amethyst Brown-dove	Raw	15.5 ± 25.1	8.47 ± 32.2	22.7 ± 22.2	24.8 ± 17.3
	Corrected	42.7 ± 25.1	24.2 ± 32.2	62.4 ± 22.2	71.3 ± 17.3
Yellow-breasted Fruit-dove	Raw	1.77 ± 51.3	3.91 ± 48.7	4.11 ± 50.3	8.21 ± 30.0
	Corrected	3.12 ± 51.3	8.58 ± 48.7	7.44 ± 50.3	16.7 ± 30.0
Guaiabero	Raw	25.1 ± 24.5	13.3 ± 32.3	6.73 ± 38.5	5.19 ± 29.3
	Corrected	33.5 ± 24.5	17.1 ± 32.3	8.90 ± 38.5	6.84 ± 29.3
Colasisi	Raw			7.43 ± 31.4	12.4 ± 27.7
	Corrected			12.5 ± 31.4	21.4 ± 27.7
Luzon Hornbill	Raw	10.9 ± 35.4	11.4 ± 29.8		
	Corrected	13.1 ± 35.4	13.5 ± 29.8		

5.5 DISCUSSION

A crucial assumption of distance sampling, including LTDS, is that samples/transects are randomly placed in the study area ensuring that animal distribution in the landscape is uniform (Buckland *et al.*, 2001, Fewster *et al.*, 2008). This uniformity assumption is clearly violated when sampling along roads or linear features where animal density is atypical. Disturbance to the animals as well as the habitat caused by hunting activities along narrow trails, and by cattle and vehicle traffic along wide roads, makes density estimates from sampling in these path types biased since one cannot assume estimates to be representative for the species and consequently cannot extrapolate results to areas larger than the area covered or survey region. Indeed, non-random transect placement in the study resulted in fewer observations nearer transect lines on hunter trails and access roads for most species, which in turn significantly reduced densities and encounter rates. The high percentage difference (118-287%) between the corrected density estimates against raw estimates highlights the significant bias of subjective placement of lines in distance sampling. This is much higher compared to the -20% bias that Marques *et al.* (2012) observed from animal avoidance of landscape features resulting to an overestimation of detection probability and underestimation of density. Large bias in density estimates was also encountered in a point transect sampling of Irish Hares *Lepus timidus hibernicus* along linear features (Marques *et al.*, 2010). Similarly, a population study of primates has produced evidence of considerable bias in density estimates on surveys that do not satisfy the uniformity assumption in survey design (Buckland *et al.*, 2010).

The higher average density of frugivores in open compared to closed forest transects in Isabela and Cagayan could be due to persistence of primary forest birds in selectively logged forests and mixed-rural habitats (Peh *et al.*, 2005). The high frugivore density in open forest may also suggest an uneven distribution of closed and open canopy transects, with the former situated mostly on the eastern side of the Sierra Madre Mountain Range which always bear the brunt of tropical typhoons that strike the country during the rainy season. Consequently, species diversity and numbers have always been low on the eastern side of the mountain range from personal observation as well as reports from local people. van Weerd and Udo de Haas (2010) found similar low bird species richness in both ultrabasic and montane forests in the Northern Sierra Madre National Park which could both be found on the eastern side of the mountain range. The southern Aurora province has a history of intensive logging 3-4 decades ago and although commercial logging still continues, it is on a much smaller scale. The abandoned logging roads have largely reverted to forest now, although some were still being used by locals to access the forest for selective logging, small-scale agriculture and hunting throughout the province. Logging has been widely known to negatively impact bird species richness and density (Marsden, 1998, Velho *et al.*, 2012) which explains the low frugivore density in logged open canopy forest in Aurora. With the government's intensive reforestation efforts in Aurora, an increase in average density of frugivores on closed canopy forest was expected as rain forest rehabilitation was shown to affect avifauna composition and abundance by making it more similar to that of naturally regenerating forest (Ansell *et al.*, 2011).

It is very important to note that it was differences in encounter rates rather than differences in detectability that were mainly responsible for differences in species density across trail types (Table 5.3). The percentage differences in ESW (effective strip width) across path types were small in all species, indicating that roads and edges created by forest trails did not alter the detectability of birds or minimally if ever. This may be due to the birds being detected mostly from aural cues whereas visual cues would be greatly affected by dense forest growth or lack thereof, as in the case of habitats surrounding access roads. Patterns of detection could therefore be different for non-calling and/or cryptic species (Dawson and Efford, 2009, Pacifici *et al.*, 2008). Encounter rate, ESW and cluster or animal group size are the three main components that affect precision in line transect abundance estimation. Conspicuousness can affect detection along transects and this was seen in increasing ESW with increasing body size e.g. 30-32 m on average for the small parrots against 72 m for the Yellow-breasted Fruit-dove. Increase in detectability was also seen with increase in body size of African savanna mammals (Ogutu *et al.*, 2006).

Path types differed in terms of floristic factors or presence of key plants and structural factors such as tree girth, canopy cover, path width and slope (Table 5.1). Among the three path types, access roads showed stark difference in structural and floristic attributes compared to the other path types in having significantly wider paths, smaller trees, gentler slope, and open canopy. Random paths and hunter trails were structurally similar and shared similar vegetation except for significantly higher occurrence of liana, rattan and Dipterocarp trees in random paths. This similarity was superficial, however, as shown by the much lower density estimates (up to 373% difference) along hunter trails compared to random paths in nine of 12 species which were even lower (up to 582% difference) than estimates along access roads. Although it must be said that frugivores were not always the target prey in hunting activities, human traffic and secondary activities such as collection of non-timber forest products along hunting trails must affect habitat use by birds. In contrast, Black-chinned Fruit-dove showed an interesting pattern of highest density (up to 430% more) along hunter trails and largest drop (up to 450% less) in effective strip width also along hunter trails. Perhaps a reason for this is the abundance of food items and other resources on edges of trails which serve to attract birds, making them more conspicuous. Another possible explanation is the fact that trails were purposely built by hunters to go through areas with perceived high density for this and other prey species. In species favouring forest edges, density estimates were much higher along access roads e.g. Guaiabero, Common Emerald Dove and Green Imperial-pigeon, although records for the latter two are too few to be conclusive. Habitat association analysis has indeed shown that the Guaiabero is tolerant of forest disturbance to a degree (Ch. 4, section 4.4.2). Some of the responses of birds and other animals to roads and forest edges have been documented elsewhere (Ortega and Capen, 2002, Yost and Wright, 2001, Marsh and Beckman, 2004).

To conclude, distance sampling can be conducted along non-random linear features but positioning samples thus causes likely bias in density estimates. It is suggested here that density estimates be adjusted with the use of a correction factor developed from an episode of robust sampling that fulfils the assumptions of the method. The density correction method has potential use in sampling other taxa in the increasingly fragmented forest landscape of the Philippines. Failure to correct for non-random sampling placement will introduce considerable bias to conservation status assessments resulting to species management and conservation programmes with ill-targeted objectives. With the constant spectre of limited conservation resources in the tropics, this is a grave mistake that ecologists and conservation workers cannot afford to make. The correction factors presented here, although not ideal, goes some way towards making population assessments more realistic where random placement of transects is prohibited by time, terrain, cost, safety, etc.

Chapter 6

THE FUTURE OF AVIAN FRUGIVORE RESEARCH AND CONSERVATION

6.1 Key findings of the dissertation research

Three major barriers to effective protected area management in the Philippines have been identified by the Protected Areas and Wildlife Bureau (PAWB) of the Department of Environment and Natural Resources (DENR): (1) poor biogeographical representation of the existing protected area (PA) system, (2) limited capacities of the DENR-PAWB and the Protected Area Management Boards (PAMB) for PA management, and (3) inadequate systems for financial planning, budgetary management and revenue generation (DENR-PAWB, 2012). The overlap between PAs and Key Biodiversity Areas identified by Conservation International is only 35% and montane areas are disproportionately represented in PA systems leaving lowland forests vulnerable to clearance from logging and agriculture (DENR-PAWB, 2012, Ambal *et al.*, 2012). Likewise, PAs in the Philippines represent only 6% of IUCN Categories I-IV protected areas (Ong *et al.*, 2002). The first two barriers stem in part from an incompletely known status and ecology of many threatened species and habitats in the Philippines (BirdLife International, 2003). This has resulted in many conservation initiatives in the country not having the benefit of baseline ecological and socio-economic research to inform conservation measures on the ground. This PhD sought not only to gather ecological data on little-known species over large geographical areas but also to develop cost-effective methods of doing ecological research in oftentimes very difficult terrain and field conditions. Each chapter's aims and major findings will be briefly discussed in turn with their conservation and future research implications.

Chapter 2. Frugivore collapse in Luzon

The chapter used data gathered from birdwatching archives, museum collection databases, unpublished expedition bird records, hunter interviews, and a 10-month bird survey in Luzon to (1) create historical and current distribution maps of frugivores in order to detect range changes (and in particular range contractions), (2) estimate population densities at a number of key sites and compare them with those of related species elsewhere in Southeast Asia, and (3) assess whether populations of frugivores in key protected areas are viable in the long term using current knowledge on likely minimum viable populations (MVPs). The following are the key findings of this chapter:

- Very little local extinction has been recorded in the last ten years, with the current survey considerably increasing the known range of some species including threatened taxa. The threatened Luzon-endemic Green Racquet-tail *Prioniturus luconensis* has been recorded from only seven sites in the last ten years.

- Ten (four parrots, five pigeons and one hornbill) out of 18 species never achieved densities of more than 5 per sq km at any site, and four (all parrots) never achieved densities of more than 1 per sq km at any site. These density estimates are much lower than densities of similar species in neighbouring Indonesia and Papua New Guinea.

- As many as eight out of 20 species, including four out of six parrots, had likely populations < 1,000 individuals in all of the five reserves considered in the study, which includes the largest reserve in the country—the Northern Sierra Madre National Park. More than one third of populations in reserves had <100 individuals. At the lowest estimate of MVP = 500 individuals, three of the smallest reserves in

Luzon are expected to lose all their frugivores and even the largest reserve will lose high proportions of its frugivore species in the next 100 years.

The many new species occurrence localities added during the study do not imply an expanding range/population but can be attributed instead to an incomplete historical record of species distribution, as museum collection expeditions were commonly to the same accessible sites (BirdLife International, 2003). The same accessibility has made these sites prone to logging and agricultural encroachment, resulting in total habitat destruction in a number of places which explains some of the local extirpations recorded in the study. This illustrates how much remains to be known of Philippine birds that records of large-bodied and charismatic species remain incomplete. The chapter also points to the importance of attempting to increase reserve size in order to increase MVPs of the most vulnerable species. One such species is the Luzon-bound Green Racquet-tail, which was recorded in only two regions during the island-wide survey and, overall, in just seven sites in the last ten years when birdwatcher and unpublished expedition reports are also taken into account, although the reasons for this ominous decline are unclear. It must be said that not only birds but the population viability of mammals and other taxa may very well be reduced by the small size of reserves and forest fragments (Burkey, 1995). Given the increasingly fragmented forests in the tropics, obtaining empirical data on population abundance and long-term viability is critical for the success of any conservation intervention.

Chapter 3. Frugivore community ecology

Non-metric multidimensional scaling ordinations were used to explore similarities between frugivore communities in 24 sites belonging to five regions in Luzon, while Mantel tests were used to explore community differences in terms of a series of geographical, habitat, and disturbance predictors. Ordinations were built both with presence/absence and population density data. The main findings of the chapter are the following:

- Clusters and outliers did not ordinate according to region, suggesting that geographical factors were not the only determinants of species occurrence and abundance.
- Consistent outliers included three sites in West Luzon and two in Central Luzon, and, in terms of species, several large rare parrots and pigeons.
- The strongest correlates of site dissimilarity were altitude and several human disturbance measures – path width, secondary forest index, canopy closure and a 'human impact index' comprising hunting, forest history and conservation management.

The archipelagic nature of the Philippines brought about by its complex geologic history has contributed to an extraordinary rate of speciation which produced many endemic species and many centres of endemism even within the island of Luzon alone (Balete *et al.*, 2009). However, frugivore community dissimilarity in the sites/reserves covered was found to be determined largely by correlates of anthropogenic disturbance apart from altitude. In the face of incomplete or nonexistent baseline ecological data on many of the protected areas in the country with which to compare, this chapter's findings flag the impact that habitat disturbance, hunting and reserve protection/management have on frugivore communities in Luzon. Southeast Asia with its largely archipelagic nature coupled with one of the highest rates of deforestation in the tropics has shown a similar pattern of biodiversity loss and decline (Sodhi *et al.*, 2010b, Turner, 1996).

Chapter 4. Frugivore habitat associations

A natural progression from the previous chapter, which explored dissimilarities in frugivore communities across Luzon's landscape, this chapter sought to establish the drivers of community composition and abundance in sites. Generalized linear mixed models were used to identify habitat associations of 18 avian frugivores in 24 sites in Luzon. Species numbers as well as species occurrence in each site were examined in relation to the effects of geographical and vegetation structures and composition. Generalised additive mixed models were then used to identify non-linear species response to habitat features. The key findings from this chapter are the following:

- Both structural and floristic variables appear to be important determinants of frugivore composition. Altitude was the strongest variable correlated with species richness and presence of most species, followed by a correlate of forest disturbance and high-altitude forest.
- Five species were high altitude specialists while six preferred lowland forest. Another six species strongly preferred primary forest while one thrives in disturbed forest.
- Species relationships with habitat variables were simple linear or quadratic except for five species that showed a non-linear response to the variables tree girth and canopy cover.

The findings will hopefully be used in capturing as much as possible the full habitat requirements of frugivores when delineating protected areas and forest corridors. Many endemic species in the Philippines are not as fortunate as knowledge on species requirements is largely missing for many species, even those threatened with extinction (Collar, 1998).

Chapter 5. Frugivore density estimation: detectability and variability with site, season and habitat type

This chapter quantified the biases that are expected to appear in estimates of species densities, encounter rates, effective strip width and overall detection function as a result of transect placement along three path categories: random paths (specially-cut transects), hunter trails (path width <100cm) and access roads (path width >100cm). The key findings of the chapter were:

- Differences in floristic and vegetation structural features as well as human disturbance in the form of hunting were responsible for the difference in species density estimates across path types. The impact that hunting has on frugivore populations is even more significant than disturbance caused by access roads in some species.
- Hunter trails yielded lowest densities and encounter rates for nine of 12 species and lowest effective strip width for seven of 12 species. Highest densities and encounter rates were along random paths for seven of 12 species.
- Differences in density across trail types were driven by differences in encounter rates rather than differences in detectability.
- Correction of density estimates from a survey with biased transect placement produced higher values with an average of 190% (118-287%) difference compared to raw estimates.

The method developed in this chapter will make biased sampling along non-random linear features possible as long as density estimates are adjusted to correct for the potentially significant bias (Marques *et al.*, 2010).

6.2 Conservation implications for Philippine frugivores

This dissertation has flagged the serious plight of the large forest frugivorous birds of Luzon, and in so doing it also suggests that the problems of population decline, range contraction and small population size are likely to affect other vertebrate taxa as well. The causes of these problems have only generally been outlined, but a combination of massive long-term habitat loss and equally chronic wildlife exploitation by local human populations seems likely to explain the phenomenon. Blueprints already exist for conservation efforts in Luzon, in the form of BirdLife International's Important Bird Areas (IBAs) and Endemic Bird Areas (EBAs), many or parts of which are not covered by any protected area (Mallari *et al.*, 2001, Chan *et al.*, 2004), and this dissertation points strongly to the need to implement these proposals in full. The fieldwork behind this dissertation also addressed four of the five unexplored forests in Luzon supporting threatened species (Mallari *et al.*, 2004), the missing site being Mt Irid-Mt Angilo which is on the southernmost part of the Sierra Madre mountain range. A notable discovery from these unexplored forests was of a small and likely highly threatened population of the Green Racquet-tail in a patch of logged forest dominated by bamboo near the foot of Mt High Peak in Zambales. Another potentially important find is of a bird-rich forest near Baler in Aurora which was the only place the Pink-bellied Imperial Pigeon *Ducula poliocephala* was recorded during the study.

However, there is also a need to re-assess how well the existing PAs represent the vast and unique biodiversity in the country. Southern Luzon has the fewest and smallest reserves in the island, the largest of which (Mt Isarog National Park) will not be able to sustain viable frugivore populations in the future apart from the common White-eared Brown-dove *Phapitreron leucotis* (Chapter 2). Likewise, the third largest reserve in the Cordillera is expected to lose all of its frugivores in the next 100 years (Chapter 2), an especially worrying situation for the island-endemic Luzon Racquet-tail, which apart from the Sierra Madre has the Cordillera supposedly as a stronghold. Reserve size has been shown in the study to influence extinction risk, as species abundance and therefore population viability are linked to it. The smallest reserves are the ones likely to suffer species loss and the ones least able to maintain viable frugivore populations. Numerous forest fragmentation and metapopulation studies have demonstrated that smaller areas are more vulnerable to habitat shrinkage and destruction and experience faster rates of species loss/extirpation (Burkey, 1995, Sodhi *et al.*, 2004b, Lundmark, 2004, Watson *et al.*, 2005). The use of biodiversity corridors may be the best means of mitigating the impacts of fragmentation not only in the nature reserve network but also in forest remnants left over from logging and destructive agricultural practices (Laurance *et al.*, 2012, Linehan *et al.*, 1995). In the Philippines, however, where land is under immense pressure both from local people for agriculture and from corporate businesses for mineral extraction, the creation of habitat corridors that allow avian populations to merge genetically is likely to be a logistical and legal challenge on a large scale.

The National Integrated Protected Areas System (NIPAS) provides for the decentralization of PA management through the instrument of the Protected Area Management Board (PAMB), a multi-stakeholder entity tasked with PA management, but this is usually seen by local communities, notably the local government, as an extension of the DENR, so they leave the responsibility for PAs with the DENR (DENR-PAWB, 2012). PA management planning is poorly institutionalized, with the quality of plans inconsistent across sites. The only biodiversity monitoring instrument for protected areas in the country (Danielsen *et al.*, 2003) has not been adequately implemented, leaving the PAMB without an objective measure for the effectiveness of PA management. Another major barrier to effective PA management in the Philippines is the bureaucratic and unsustainable financial systems governing PAs which do not provide for sufficient generation and management of revenue for PA operation (DENR-PAWB, 2012).

These are just some of the factors that contribute to the ineffectiveness of PA management, which is manifest in nonexistent or insufficient patrols for biodiversity monitoring as well as for controlling wildlife exploitation and habitat destruction within PAs. There is a pressing need for PA management programmes to put a far greater emphasis on curbing further habitat disturbance/destruction and hunting within reserves, as these are negatively influencing frugivore communities and potentially disrupting seed dispersal and forest regeneration dynamics. This is especially important in the largest reserves, which represent the country's best chance of retaining viable frugivore populations.

That the Luzon-bound and threatened/near-threatened Green Racquet-tail, Luzon Racquet-tail *Prioniturus montanus* and Flame-breasted Fruit-dove *Ptilinopus marchei* were recorded in fewer than fifteen localities each and in very low densities in all of Luzon underscores the urgent need for conservation intervention for these as well as other island endemics. The future is especially dire for the Green Racquet-tail, which has a population of under 250 individuals in the largest reserve (NSMNP) in the country—a situation that qualifies it for the Endangered category of threat in the following criteria: B1ab, C2ai (IUCN Standards and Petitions Subcommittee, 2013). Population or range contraction for the species cannot be accurately inferred as the historical record is incomplete.

In the end, research-based conservation intervention is not all that is needed. A coal-fired power plant has just been given a permit to operate very near Rasa Island, one of the last strongholds of the Philippine Cockatoo *Cacatua haematuropygia* in the country, by the Palawan Council for Sustainable Development (PCSD), despite opposition from the local government as well as recommendations against its operation by its own technical evaluators (Anda, 2013). The Katala Foundation, a non-government organization that has laboured for Philippine Cockatoo conservation for many years, has exposed corruption in the leadership of the PCSD as the cause of this blatant disregard for expert technical and scientific evidence on the impact the power plant will have on the Philippine Cockatoo population. It is this kind of weak implementation of environmental laws that erode best-laid conservation programmes and initiatives in the country.

6.3 Implications for future study methods

A hopefully valuable contribution of this dissertation research was to quantify and correct for bias in species density estimates caused by non-random placement of transects, thus making it possible to conduct surveys along transects with varying path widths and degrees of disturbance (Marques *et al.*, 2010, Marques *et al.*, 2012). Use of the method is not limited to the study of birds, as other taxa that are amenable to transect sampling in population studies would benefit from the density-correction system described in this study. This is especially useful to transect-based wildlife surveys in the tropics where a random placement of transects is constrained by time, terrain, cost, safety, etc. The relevance of this method to adjust estimates of density in surveys conducted in non-ideal field conditions is becoming more apparent in the increasingly fragmented forests and habitats not only in the Philippines but in the wider tropics (Brooks *et al.*, 1999, Castelletta *et al.*, 2005, Korfanta *et al.*, 2012, Laurance, 1999, Tanner and Kirk, 2008).

6.4 Future research and conservation priorities

- There is need for a thorough and systematic search for the remaining sites where the Luzon-endemic Green Racquet-tail, Luzon Racquet-tail and Flame-breasted Fruit-dove survive in order that relevant and timely conservation measures or intervention can be devised. A crucial first measure is to stem deforestation and curb hunting activities in sites that are known habitat of the species. This can be facilitated by community-based species management and monitoring programmes at sites where the species are especially vulnerable. Complementary conservation education campaigns will help ensure the success of the programmes in the long-term. Protection of the species can be institutionalised through provincial, municipal and even barangay/village level ordinances and declaration of local protected areas.

- In spite of the high rate of deforestation in the Philippines, species discovery in the country is also one of the highest in the world with 270 species discovered in the past 25 years—not including insects, marine life, and those species awaiting description (de Leon and Lita, 2012). Future expeditions must be organized to little explored forests in the Philippines with the objective of not only completely documenting biodiversity in these places but also of obtaining solid evidence of their abundance (Mallari *et al.*, 2004, Mallari *et al.*, 2001). With the steady encroachment of logging, development and agriculture into the last remaining forests of the Philippines, the chances of species being lost without ever having been discovered become higher with each passing year.

- The country's highly fragmented forest landscapes and many centres of endemism lend themselves well to metapopulation and disturbance gradient studies which are based on accurate species occurrence data and abundance estimates. They represent a potential laboratory for measuring the impacts of disturbance and isolation on species and populations and for identifying the consequences for the ecosystem services of seed dispersal and forest regeneration. Key points for investigation include an assessment of the number of subpopulations in the landscape, species tolerance to disturbance and dispersal abilities of species across an increasingly expanding human-altered landscape.

- The incredibly depauperate state of knowledge on Philippine frugivores (Collar, 1998, Walker, 2007) and biodiversity in general (BirdLife International, 2003) is due in part to lack in capacity for sound ecological research in the country. Since 1950, 88 papers on Philippine birds worthy of listing in Web of Science were published, with only 18 papers on bird ecology (less than one paper every 3.5 years). Moreover, around three quarters of these papers were authored by non-Filipinos. This is evidence of a major deficiency in the country's technical and professional ability to manage the environment and to conserve biodiversity. Incidentally, American and European researchers also dominated ecological research publications coming out of the Andes and the Amazon (Pitman *et al.*, 2011). A wider review covering 1333 ecological papers from tropical countries in the period 1995 to 2004 shows the same pattern of unequal geographical distribution of research in the tropics with lead authors mostly from a developed country (Stocks *et al.*, 2008). A mechanism for research capacity-building and training of Filipino biologists will greatly benefit conservation initiatives on the ground by making it more cost-effective, sustainable and potentially more socially acceptable and participatory. Collaborative research programs must be designed where visiting foreign researchers work closely with in-country collaborators thereby offering opportunities for training of young undergraduate and graduate-level Filipino biologists in data analysis and manuscript preparation and not just fieldwork. Local institutions that employ biologists must be strengthened to provide scientists with the incentive to stay in the country once they are established researchers.

- Building on the previous point, emphasis must be put on basic ecological research in order to further our understanding of the food, habitat and breeding requirements of the many unique bird species in the country. If baseline information is missing for even birds which are mostly diurnal and arguably easier to study, one can only surmise on the amount of ecological information missing for other Philippine endemic taxa.

PA management and conservation initiatives in the Philippines have always been saddled by contradictory and ill-defined laws relating to land tenure, poor government management of poverty-stricken and displaced human communities, powerful lobbies from the corporate sector, institutional corruption and inertia, and widespread indifference to the plight of wildlife and the environment. In spite of these disheartening conditions, hope comes in trickles as small conservation victories are won through much hard work, dedication and dialogue with the aim of finding a balance between the oftentimes conflicting interests of development and environmental protection (Posa *et al.*, 2008).

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Appendix 2.1. Survey areas per region in Luzon with total transect length, altitudinal range, protection status and predominant habitat type per site. Kaingin = swidden or slash-and-burn agriculture. DENR = Department of Energy and Natural Resources. PAMB = Protected Area Management Board.

Areas per region	Dates	Kilometres walked (transects)	Altitudinal sampling range (m asl)	Protection status	Predominant habitat type
Central Luzon					
Mounts Banahaw-San Cristobal Protected Landscape, Quezon	14-23 May 2010	32.4 (15)	580-1935	Active volunteer forest guards ensure reserve is protected from mining and logging activities but kaingin farming continues to encroach	Regenerating secondary forest in the low elevations and mixed evergreen-gymnosperm and mossy forests toward the peak
Burdeos, Polillo Island, Quezon	9-11 June 2010	26.8 (9)	5-200	Volunteer forest guides struggle to keep regular patrols and feel disempowered to prevent logging and kaingin activities	Mangrove forest at sea-level and degraded secondary forest with selective logging and extensive kaingin farming
Quezon Protected Landscape, Quezon	7-10 July 2010	22 (10)	25-355	Volunteer forest guards involved in reforestation and patrol of the reserve but kaingin farming and hunting continues in the buffer zone	Regenerating lowland dipterocarp forest over limestone
Cordillera					
Mt. Polis, Barangays Cambulo and Pula, Cordillera Administrative Region	20-26 July 2010	22 (6)	1155-1895	Forest at high altitudes protected by locals as watershed; hunting is prevalent and is a way of life for all males from pre-puberty	Highly agricultural landscape in the lowlands and mixed pine-evergreen and mossy forests confined near the peak
Balbalasang-Balbalan National Park, Kalinga	29 July-3 August 2010	34.8 (12)	900-1850	Flat lands are highly agricultural while forested mountains are protected as source of wood and traditional hunting ground	Extensive old-growth evergreen forest dominated by *Agathis* at higher elevations and mixed grass-pine forest in the lowlands
Calanasan, Apayao	10-13 August 2010	19.2 (8)	665-1060	Kaingin farming in flat land; mayor banned hunting of rufous hornbills for ten years to allow the population to recover	Good secondary forest starting from the lowlands to montane elevations where trees are stunted and gnarled

Appendix 2.1 continued

Areas per region	**Dates**	**Kilometres walked (transects)**	**Altitudinal sampling range (m asl)**	**Protection status**	**Predominant habitat type**
Sierra Madre					
Divilacan, Maconacon and San Pablo, Isabela	17 February-5 March 2010	50 (28)	10-1270	Dicatian Lake and forest surrounding it is protected by a municipal ordinance and a conservation NGO; illegal logging continues and has left the western side of the Sierra Madre barren	Beach forest along the coast, regenerating secondary forest in the lowlands, old-growth dipterocarp forest in the Sierra Madre interior and mossy forest along mountain ridges
Mt Cetaceo, Peñablanca, Cagayan	13-20 March 2010	37.6 (12)	320-1110	The area is protected by an indigenous tribe for hunting purposes, but lowland settlers are slowly clearing the edges for farming	Regenerating logged-over forest dominated by medium-sized trees and overrun by tall grass and woody vines in forest gaps and along old logging trails
Baler, San Luis, Dilasag, Casiguran and Dinalungan, Aurora	25 August-19 September 2010	114.4 (47)	10-1190	Commercial logging continues along the border between Isabela and Aurora but is banned elsewhere. Some selective logging and hunting continues; DENR has a programme to reforest logging remnants	Regenerating logged-over forest throughout Aurora province with agricultural plantations along the coast and generally untouched montane/mossy forest at higher elevations
South Luzon					
Mt Malinao, Diaro, Albay	17-18 April 2010	8 (2)	490-1140	Kaingin farming gradually extends from the lowlands up the mountain	Extensive abaca plantation in the lower elevations and forest gaps replaced by secondary forest and mossy forest higher up
Caramoan National Park, Camarines Sur	22-24 April 2010	22 (10)	20-205	PAMB is powerless against development activities of individuals within the reserve	A mixed forest-agricultural landscape over limestone bordered by the sea
Mt. Isarog National Park, Naga, Camarines Sur	27 April-3 May 2010	32.4 (11)	295-1760	PAMB strictly enforces a logging ban although hunting remains unchecked; kaingin farming continues to encroach in the lower areas of the reserve	Highly agricultural in the lowlands and gradually giving way to mature secondary forest and old-growth mossy forest toward the peak

Appendix 2.1 continued

Areas per region	**Dates**	**Kilometres walked (transects)**	**Altitudinal sampling range (m asl)**	**Protection status**	**Predominant habitat type**
West Luzon					
Mt Tapulao and areas around it, Zambales	21 January-1 February 2010	30.8 (21)	235-1970	Contested mining operation near the peak; rampant selective logging and kaingin farming	Scrub/bamboo and highly fragmented secondary forest in the lowlands to mixed evergreen-gymnosperm and dwarf mossy forests toward the peak
Subic Watershed Forest Reserve (SWFR) and Bataan National Park (BNP), Bataan	10-30 December 2010	44.4 (22)	20-430	Paid full-time forest guards in the SWFR and volunteer forest guards in BNP; selective logging in BNP and hunting for bush meat in both SWFR and BNP	Regenerating logged-over forest dominated by dipterocarps in the upper elevations and mixed bamboo-evergreen stand in the lower elevations

Appendix 2.2 Number of encounters of each species, transect length (km), overall encounter rate (individuals km $^{-1}$; sites combined), and species richness and evenness in surveyed sites in Luzon, Philippines. Both an observed (Obs) species richness and one estimated (Est) using the Chao2 estimator of EstimateS along with associated 95% confidence intervals are shown.

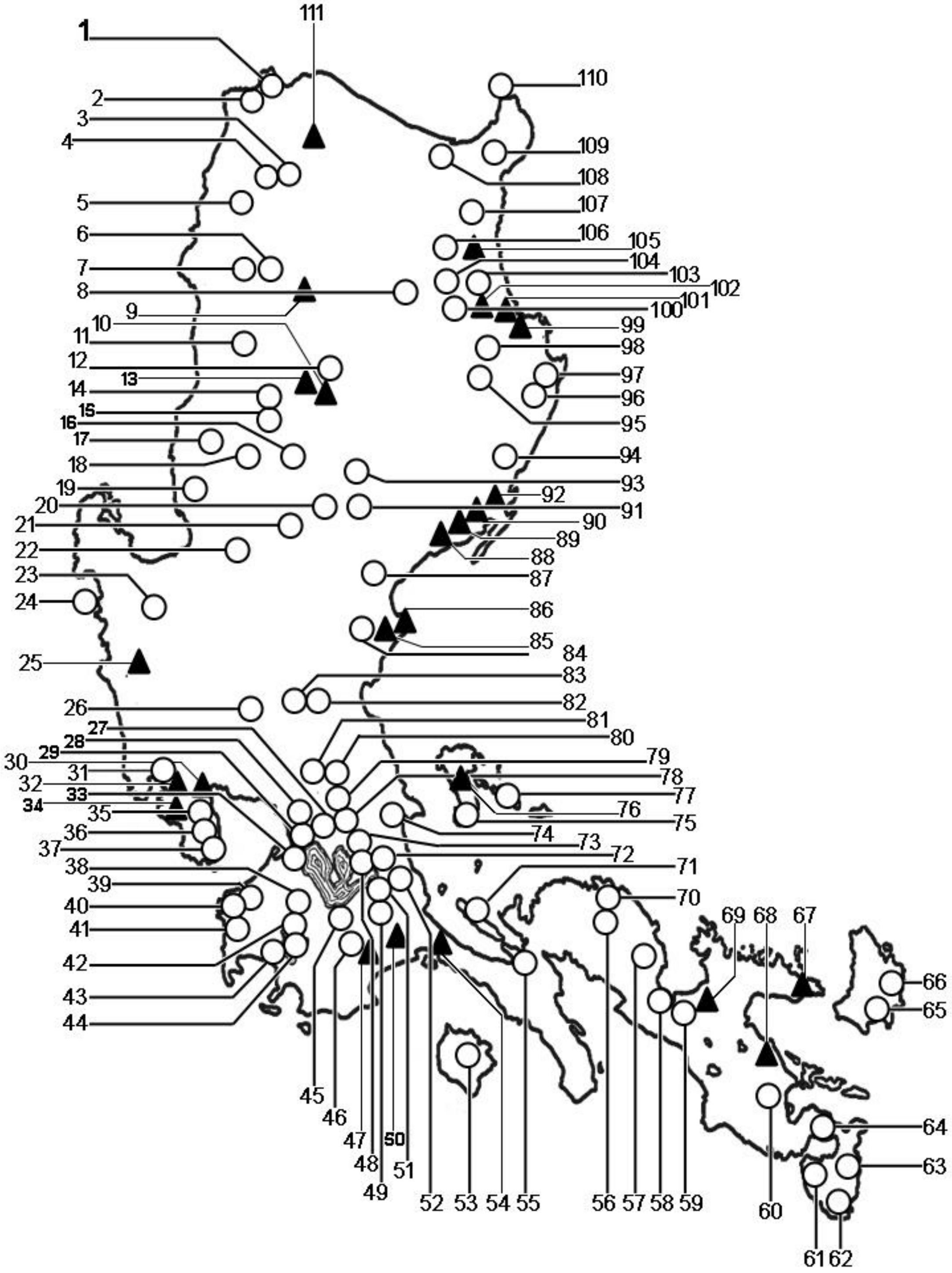
	km	TRPO	PHLE	PHAM	PTMA	PTME	PTOC	PTLE	DUPO	DUCA	DUAE	COVI	MATE	CHIN	GALU	BOLU	TALU	PRLU	PRDI	PRMO	LOPH	PEMA	BUHY	Species richness (95% CI)		Species evenness
																								Obs	Est	
WEST LUZON																										
Zambales	30.8		105	1	1		110	44			3		52	6	1	43		8			18	10	7	14	19 (14-55)	0.74
Bataan	44.4	4	110	23		1	6	1			9		8	5	1	122	10	13			29	34	13	16	17 (16-24)	0.72
CENTRAL LUZON																										
Banahaw	32.4		130	3	15		5						91	1	5	6					25	2		10	10 (10-10)	0.62
Polillo	26.8			30		3	2	13			21		1	65	17		2				1	26		11	11 (11-14)	0.76
Quezon PL	22.0		83	18		9	3	10						12	12	5					6	31	6	11	11 (11-11)	0.79
SOUTH LUZON																										
Malinao	8.0		32	6		3	8						29	1		21					4	1		9	10 (9-22)	0.78
Caramoan	22.0	2	130	1		1	9			1	23			3	9	20			11		2	17		13	13 (13-19)	0.61
Isarog	32.4		186	13			22					2	39	7	7	29					2	5		10	10 (10-10)	0.57
SIERRA MADRE																										
Isabela	50.0		81	206	1	12	10	1		6			2	1	7	21		1		4	25	18	48	16	20 (17-45)	0.64
Cagayan	37.6		318	93		43	96	12		2			15	30	21	21		1			38	22	32	14	15 (14-28)	0.74
Aurora	114.4		379	124	13	22	39	23	3		1		3	19	4	80					18	50	88	15	15 (15-15)	0.70

Appendix 2.2 continued

	km	TRPO	PHLE	PHAM	PTMA	PTME	PTOC	PTLE	DUPO	DUCA	DUAE	COVI	MATE	CHIN	GALU	BOLU	TALU	PRLU	PRDI	PRMO	LOPH	PEMA	BUHY	Species richness (95% CI)		Species evenness
																								Obs	Est	
CORDILLERA																										
Ifugao	22.0		12	6	2	1							1		1					2	7			8	9 (8-18)	0.81
Kalinga	34.8		17	9	24			2					2	5	26					10	6	1	17	11	11 (11-19)	0.87
Apayao	19.2		21	16	9	3	1	4					2	2	1					1	5	3	14	13	14 (13-21)	0.82
TOTAL	496.8	6	1604	549	65	98	289	110	3	9	57	2	245	157	112	368	12	23	11	17	186	220	228			
Encounter Rate		0	3.2	1.1	0.1	0.2	0.6	0.2	0	0	0.1	0	0.5	0.3	0.2	0.7	0	0	0	0	0.4	0.4	0.5			

TRPO=pompadour green-pigeon *Treron pompadora*, **PHLE**=white-eared brown-dove *Phapitreron leucotis*, **PHAM**=amethyst brown-dove *Phapitreron amethystina*, **PTMA**=flame-breasted fruit-dove *Ptilinopus marchei*, **PTME**=cream-bellied fruit-dove *Ptilinopus merrilli*, **PTOC**=yellow-breasted fruit-dove *Ptilinopus occipitalis*, **PTLE**=black-chinned fruit-dove *Ptilinopus leclancheri*, **DUPO**=pink-bellied imperial-pigeon *Ducula poliocephala*, **DUCA**= spotted imperial-pigeon *Ducula carola*, **DUAE**=green imperial-pigeon *Ducula aenea*, **COVI**= metallic pigeon *Columba vitiensis*, **MATE**=Philippine cuckoo-dove *Macropygia tenuirostris*, **CHIN**=common emerald dove *Chalcophaps indica*, **GALU**=Luzon bleeding-heart *Gallicolumba luzonica*, **BOLU**=guaiabero *Bolbopsittacus lunulatus*, **TALU**=blue-naped parrot *Tanygnathus lucionensis*, **PRLU**=green racquet-tail *Prioniturus luconensis*, **PRDI**=blue-crowned racquet-tail *Prioniturus discurus*, **PRMO**=Luzon racquet-tail *Prioniturus montanus*, **LOPH**=colasisi *Loriculus philippensis*, **PEMA**=Luzon hornbill *Penelopides manillae*, **BUHY**=rufous hornbill *Buceros hydrocorax*

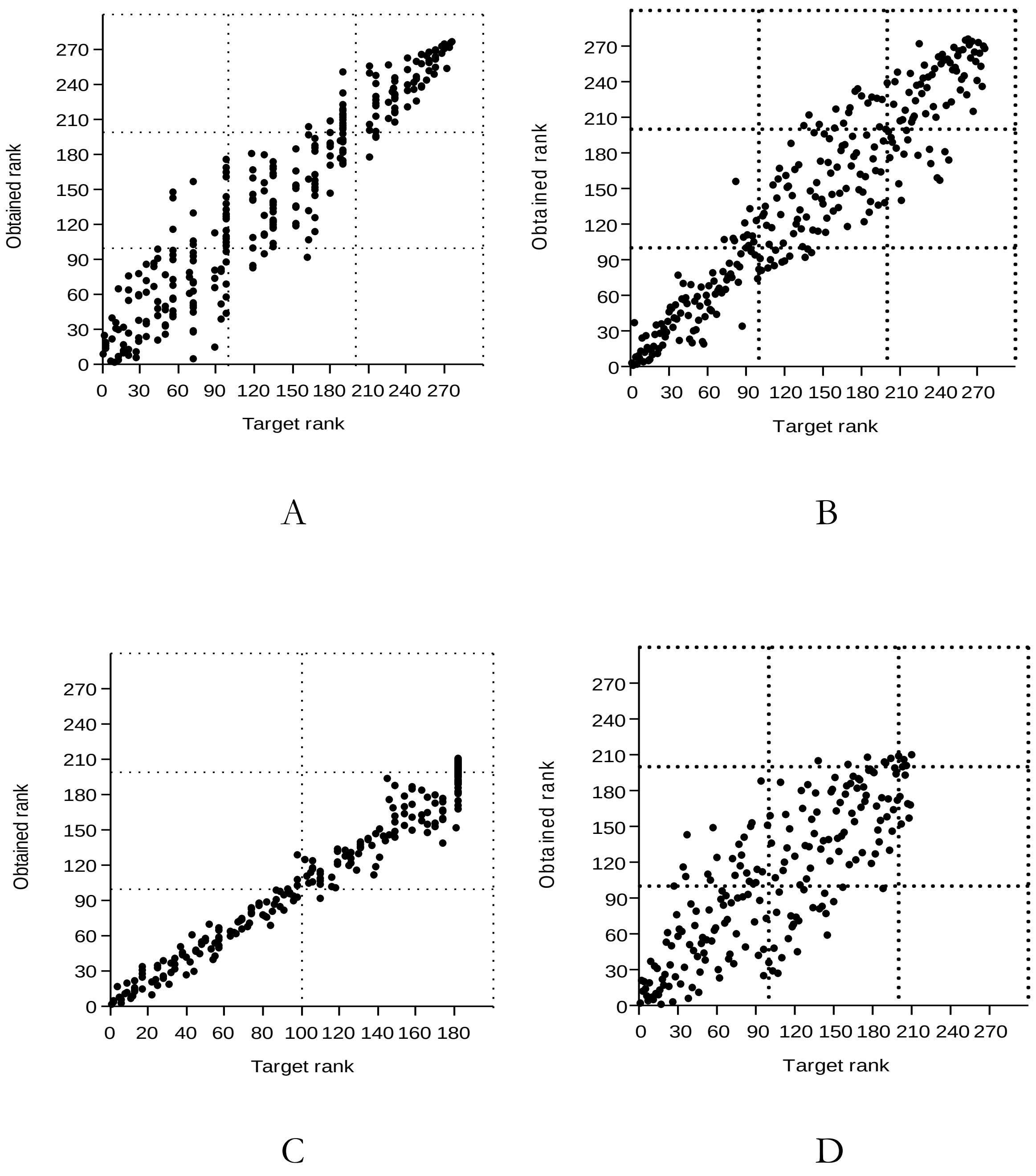
Appendix 2.3. Sites used for analysis of frugivore distribution in Luzon. Triangles indicate sites visited in the current survey.



(1) Bangui, Ilocos Norte; (2) Pagudpud, Ilocos Norte; (3) Mt. Sicapo-o, Mt. Simminublan, Ilocos Norte; (4) Solsona, Ilocos Norte; (5) Simminaplan, Ilocos Norte; (6) Massisiat, Abra; (7) Bucay, Abra; (8) Liwan (Rizal), Kalinga; (9) Balbalasang-Balbalan National Park, Kalinga; (10) Cambulo, Ifugao; (11) Barit, Abra; (12) Barlig, Mountain Province; (13) Mt. Polis, CAR; (14) Bauko, Mountain Province; (15) Mt. Data National Park, Mountain Province; (16) Mt. Pulog National Park; (17) Sablan, Benguet; (18) Atok, Benguet; (19) Baguio City, Benguet; (20) Dupax, Nueva Vizcaya; (21) Dalton Pass and Imugan, Nueva Vizcaya; (22) San Miguel, Pangasinan; (23) Manleluag Hot Springs National Park, Pangasinan; (24) Hermana Mayor island, Zambales; (25) Mt. Tapulao, Zambales; (26) Mt. Arayat, Pampanga; (27) Valley Golf, Antipolo, Rizal; (28) Quezon City, Metro Manila; (29) Makati, San Miguel, Taguig and Pateros, Metro Manila; (30) Mt. Natib, Orani, Bataan; (31) Olongapo City, Zambales; (32) Subic Watershed Forest Reserve; (33) Parañaque and Muntinlupa, Metro Manila; (34) Bataan National Park, Morong, Bataan; (35) Samal, Bataan; (36) Mt. Samat and Mt. Mariveles, Bataan; (37) Mt. Cayapo, Limay, Bataan; (38) Silang, Cavite; (39) Caylabne Bay Resort, Ternate, Cavite; (40) Mt. Palay-palay-Mataas na Gulod National Park, Cavite; (41) Nasugbu, Batangas; (42) Tagaytay Highlands, Cavite; (43) Leisure Farms, Lemery, Batangas; (44) Bubuin and Napayung Islands, Taal Lake, Batangas; (45) Mt. Makiling National Park, Laguna; (46) Sampaloc Lake and Villa Escudero, San Pablo, Laguna; (47) Mts. Banahaw-San Cristobal Protected Landscape, Dolores, Quezon; (48) Jala-jala and Pililla, Rizal; (49) Majayjay, Laguna; (50) Mts. Banahaw-San Cristobal Protected Landscape, Tayabas, Quezon; (51) Lumban, Laguna; (52) Kalayaan, Laguna; (53) Marinduque; (54) Quezon Protected Landscape, Quezon; (55) Lopez, Quezon; (56) Mt. Labo, Camarines Norte; (57) Bicol National Park, Camarines Norte and Sur boundary; (58) Cabusao, Camarines Sur; (59) Magarao, Camarines Sur; (60) Guinobatan, Albay; (61) Bulan, Sorsogon; (62) Matnog, Sorsogon; (63) Mt. Bulusan, Sorsogon; (64) Guinlajon, Sorsogon; (65) Bato, Catanduanes; (66) Viga-Gigmoto Watershed, Catanduanes; (67) Caramoan National Park, Camarines Sur; (68) Mt. Malinao, Albay; (69) Mt. Isarog National Park, Camarines Sur; (70) Panganiban, Camarines Norte; (71) Alabat, Quezon; (72) Santa Maria, Famy, Siniloan, Pakil, Pangil and Paete, Laguna; (73) Tanay, Rizal; (74) Real, Quezon; (75) Polillo, Quezon; (76) Burdeos, Quezon; (77) Patnanungan Island, Quezon; (78) Boso-boso, Antpolo, Rizal; (79) Montalban (Rodriguez), Rizal; (80) Ipo and Angat Dams; (81) mountain north-east of Bayabas, (82) Papaya, Nueva Ecija; (83) Gapan, Nueva Ecija; (84) Aurora Memorial National Park, Aurora; (85) Mt. Cabulao, San Luis, Aurora; (86) Baler, Aurora; (87) Tabayong River, border of Quirino and Aurora; (88) Simbahan-Talagas Protected Landscape, Aurora; (89) Talaytay Protected Landscape; (90) Calabgan Watershed Forest Reserve; (91) Casibo, Nueva Vizcaya; (92) Casapsapan Beach and Amro River Watershed Forest Reserve, Aurora; (93) Quezon, Nueva Vizcaya; (94) Diagopanay, Dinapigue, Isabela; (95) San Mariano, Isabela; (96) Mt. Dipalayag, San Mariano, Isabela; (97) Mt. Palanan, Isabela; (98) Minuma and Siagot, Ilagan, Isabela; (99) Divilacan, Isabela; (100) Masipi, Isabela; (101) Maconacon, Isabela; (102) San Pablo, Isabela; (103) Mt. Dos Los Cuernos, Peñablanca, Cagayan; (104) Palay and Cayapa, Peñablanca, Cagayan; (105) Mt. Cetaceo, Peñablanca, Cagayan; (106) Quibal, Peñablanca, Cagayan; (107) Baggao, Cagayan; (108) Mt. Tabuan, Cagayan; (109) Mt. Cagua, Gonzaga, Cagayan; (110) Palaui Island, Sta. Ana, Cagayan; (111) Calanasan, Apayao.

Data came from published papers, birdwatching lists from the Wild bird Club of the Philippines (http://www.birdwatch.ph/html/record/record.html), Dr Nigel Collar's list of bird records from several museums including the Philippine National Museum (PNM), the unpublished expedition reports of Arne Jensen (1994) plus records held in the following institutions and accessed through the ORNIS data portal (http://ornisnet.org) on May 2011: Academy of Natural Sciences, Philadelphia, PA (ANSP); American Museum of Natural History, New York, NY (AMNH); Yale University Peabody Museum, New Haven, CT (YPM); Delaware Museum of Natural History, Wilmington, DE (DMNH); Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ); Western Foundation of Vertebrate Zoology, Camarillo, CA (WFVZ); Kansas University Natural History Museum, Lawrence, KS (KU); United States National Museum, Washington, D.C. (USNM); Field Museum of Natural History, Chicago, IL (FMNH); California Academy of Sciences, San Francisco, CA (CAS); Museum of Vertebrate Zoology, University of California, Berkeley, CA (MVZ); Denver Museum of Nature and Science, Denver, CO (DMNS); University of Michigan, Museum of Zoology, Ann Arbor, MI (UMMZ); Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM (MSB); Burke Museum of Natural History, University of Washington, Seattle, WA (UWBM); Bishop Museum of Natural History, Honolulu, HI (BPBM); University of Arizona Bird Collection, Tucson, AZ (UAZ); James R. Slater Museum of Natural History, University of Puget Sound, Tacoma, WA (PSM).

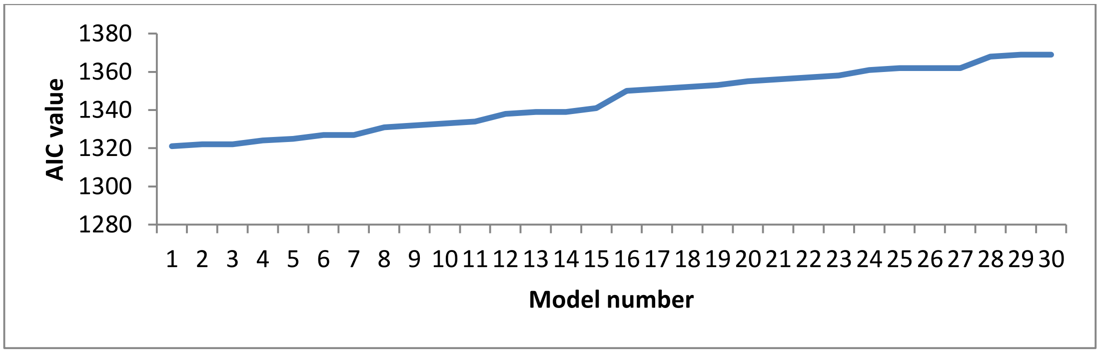
Appendix 3.1 Shepard diagrams of the following NMDS analyses: A – ordination of sites based on presence-absence data; B – ordination of sites based on standardized species density; C – ordination of species based on presence-absence; D – ordination of species based on standardized species density.



Appendix 4.1 AIC scores for all GLMMs. + and – denote the variables included in models with positive and negative coefficients or relationships respectively. * $p < 0.05$; ** $p < 0.005$; *** $p < 0.0005$

1. White-eared Brown-dove *Phapitreron leucotis*

AvAlt	AvCCover	Factor 1	AvPath	AvGirth	AIC	ΔAIC
– ***	+***	– **		+	1320	0
– ***	+***	– **			1321	1
– ***	+***	– **	–	+	1322	2
– ***	+***	– **	–		1322	2
– ***	+***			+	1324	4
– ***	+***				1325	5
– ***	+***		–		1327	7
– ***	+***		–	+	1327	7
– ***		– **	–	+	1331	11
– ***		– **		+	1332	12
– ***		– **	–		1333	13
– ***		– **			1334	14
– ***		–		+	1338	18
– ***			–		1339	19
– ***				+	1339	19
– ***					1341	21
	+***	– **			1350	30
	+***	– **		+	1351	31
	+***	– **	–		1352	32
	+***	– **	–	+	1353	33
	+***				1355	35
	+***			+	1356	36
	+***		–		1357	37
	+***		–	+	1358	38
		– **	–		1361	41
		– **			1362	42
		– **		+	1362	42
		– **	–	+	1362	42
			–		1368	48
				+	1369	49
			–	+	1369	49

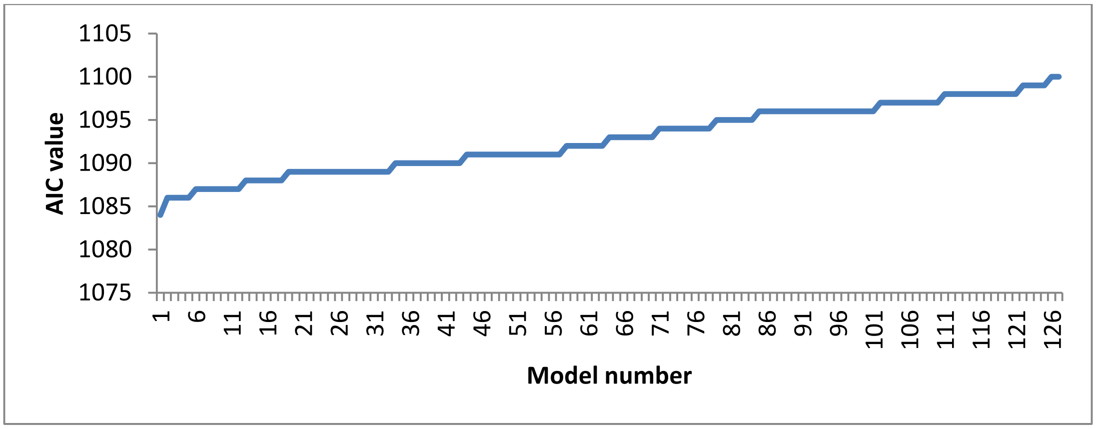


2. Amethyst Brown-dove *Phapitreron amethystinus*

AvPath	AvGirth	AvSlope	CCover	Factor1	Factor2	Factor3	AIC	ΔAIC
	+**			+*		+*	1084	0
–	+**			+*		+*	1086	2
	+**	–		+*		+*	1086	2
	+**		–	+*		+*	1086	2
	+**			+*	–	+	1086	2
	+**				–		1087	3
	+**					+	1087	3
	+**			+	–		1087	3
	+**				–	+	1087	3
–	+**		–	+*		+*	1087	3
–	+**			+*	–	+	1087	3
	+**		–	+	–	+*	1087	3
	+**						1088	4
	+**			+			1088	4
	+**		–			+	1088	4
–	+**	–		+*		+*	1088	4
	+**	–	–	+*		+*	1088	4
	+**	–		+	–	+	1088	4
–	+**				–		1089	5
–	+**					+	1089	5
	+**	–			–		1089	5
	+**	–				+	1089	5
	+**		–	+			1089	5
	+**		–		–		1089	5
–	+**			+	–		1089	5
–	+**				–	+	1089	5
	+**	–		+	–		1089	5
	+**	–			–	+	1089	5
	+**		–	+	–		1089	5
	+**		–		–	+	1089	5
–	+**	–	–	+*		+*	1089	5
–	+**	–		+*	–	+	1089	5
–	+**		–	+	–	+*	1089	5
	+**	–	–	+	–	+*	1090	6
–	+**						1090	6
	+**	–					1090	6
	+**		–				1090	6
–	+**			+			1090	6
	+**	–		+			1090	6
–	+**		–		–		1090	6
–	+**		–			+	1090	6
	+**	–	–		–		1090	6
	+**	–	–			+	1090	6
–	+**		–		–	+	1091	7
				+*		+*	1091	7
–	+**		–				1091	7
–	+**	–		+			1091	7
–	+**	–			–		1091	7

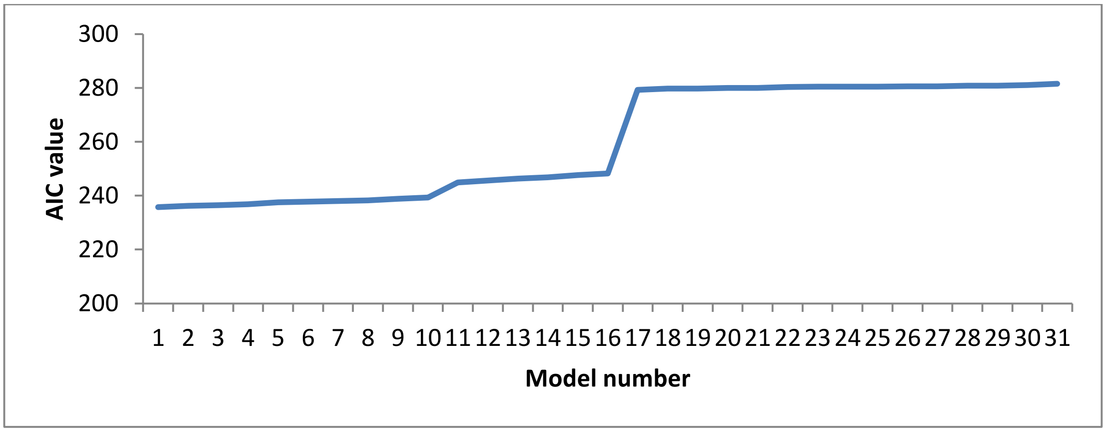
AvPath	AvGirth	AvSlope	CCover	Factor1	Factor2	Factor3	AIC	ΔAIC
–	+**	–				+	1091	7
–	+**		–	+			1091	7
	+**	–	–	+			1091	7
–	+**	–		+	–		1091	7
–	+**	–			–	+	1091	7
–	+**		–	+	–		1091	7
	+**	–	–	+	–		1091	7
	+**	–	–	–		+	1091	7
–	+**	–	–	+	–	+*	1091	7
–	+**	–					1092	8
	+**	–	–				1092	8
				+	–	+	1092	8
–	+**	–	–		–		1092	8
–	+**	–	–			+	1092	8
–	+**	–	–		–	+	1092	8
					–		1093	9
–				+*		+*	1093	9
		–		+*		+*	1093	9
			–	+*		+*	1093	9
–	+**	–	–				1093	9
–	+**	–	–	+			1093	9
–	+**	–	–	+	–		1093	9
				+			1094	10
						+	1094	10
				+	–		1094	10
					–	+	1094	10
–			–	+*		+*	1094	10
–				+*	–	+	1094	10
		–		+	–	+	1094	10
			–	+	–	+	1094	10
–					–		1095	11
		–			–		1095	11
			–		–		1095	11
			–			+	1095	11
–				+	–		1095	11
–		–		+*		+*	1095	11
		–	–	+*		+*	1096	12
–							1096	12
		–					1096	12
			–				1096	12
–				+			1096	12
–						+	1096	12
		–		+			1096	12
		–				+	1096	12
			–	+			1096	12
–					–	+	1096	12
		–		+	–		1096	12
		–			–	+	1096	12
			–	+	–		1096	12
			–		–	+	1096	12

AvPath	AvGirth	AvSlope	CCover	Factor1	Factor2	Factor3	AIC	ΔAIC
–		–	–	+*		+*	1096	12
–		–		+*	–	+	1096	12
–			–	+	–	+	1096	12
		–	–	+	–	+	1097	13
–		–			–		1097	13
–			–		–		1097	13
–			–			+	1097	13
		–	–		–		1097	13
		–	–			+	1097	13
–		–		+	–		1097	13
–			–	+	–		1097	13
–			–		–	+	1097	13
–		–					1098	14
–			–				1098	14
		–	–				1098	14
–		–		+			1098	14
–		–				+	1098	14
–			–	+			1098	14
		–	–	+			1098	14
–		–			–	+	1098	14
		–	–	+	–		1098	14
		–	–		–	+	1098	14
–		–	–	+	–	+	1098	14
–		–	–		–		1099	15
–		–	–			+	1099	15
–		–	–	+	–		1099	15
–		–	–		–	+	1099	15
–		–	–				1100	16
–		–	–	+			1100	16



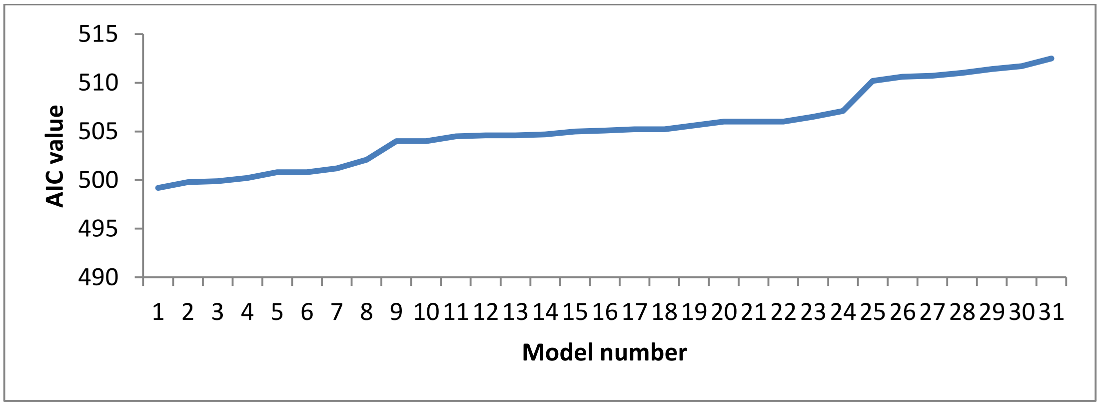
3. Flame-breasted Fruit-dove *Ptilinopus marchei*

AvAlt	AvPath	Factor 3	AveSlope	Factor 1	AIC	ΔAIC
+***			–		235.8	0.0
+***	–			–	236.2	0.4
+***			–	–	236.5	0.7
+***	–		–		236.8	1.0
+***	–		–	–	237.5	1.7
+***		–	–		237.8	2.0
+***	–	–		–	238.0	2.2
+***		–	–	–	238.3	2.5
+***	–	–	–		238.8	3.0
+***	–	–	–	–	239.3	3.5
+***	–				244.9	9.1
+***				–	245.6	9.8
+***					246.3	10.5
+***	–	+			246.8	11.0
+***		–		–	247.6	11.8
+***		+			248.2	12.4
	–	+			279.3	43.5
	–				279.7	43.9
		+			279.8	44.0
	–			–	280.0	44.2
		+	–		280.0	44.2
	–	+	–		280.3	44.5
			–		280.5	44.7
	–		–		280.5	44.7
	–	+		–	280.5	44.7
				–	280.6	44.8
			–	–	280.6	44.8
		+		–	280.8	45.0
	–		–	–	280.8	45.0
		+	–	–	281.1	45.3
	–	+	–	–	281.5	45.7



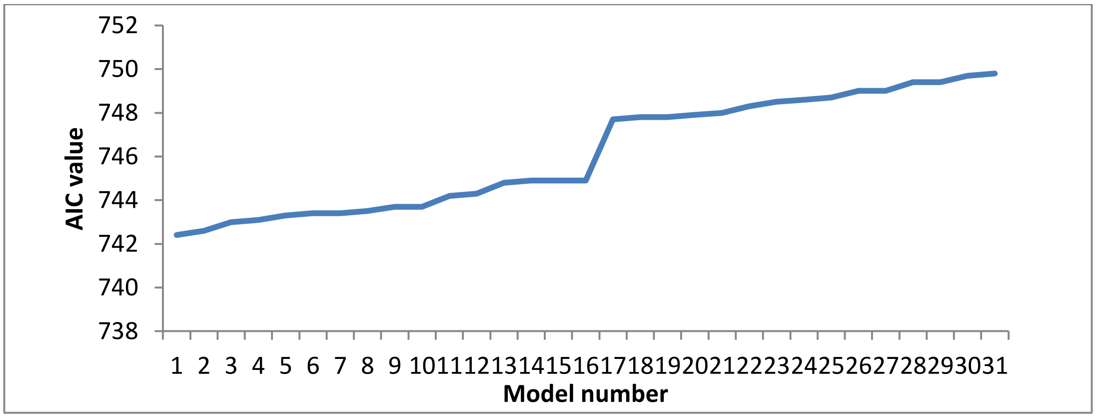
4. Cream-bellied Fruit-dove *Ptilinopus merrilli*

AvAlt	AvGirth	Factor 1	Factor 3	AveSlope	AIC	ΔAIC
+**	+**				499.2	0
+**	+**	+			499.8	0.6
+**	+**				499.9	0.7
+**	+*	–			500.2	1.0
+**	+*	+		–	500.8	1.6
+**	+*		–	–	500.8	1.6
+**	+**	+	–		501.2	2.0
+**	+*	+	–	–	502.1	2.9
+**					504.0	4.8
	+**				504.0	4.8
	+**	+			504.5	5.3
+**		+			504.6	5.4
+**				–	504.6	5.4
+**			–		504.7	5.5
	+**		–		505.0	5.8
+**			–	–	505.1	5.9
	+**			–	505.2	6.0
+**		+		–	505.2	6.0
	+**	+		–	505.6	6.4
+**		+	–		506.0	6.8
	+**	+	–		506.0	6.8
	+**	–		–	506.0	6.8
+**		+	–	–	506.5	7.3
	+**	+	–	–	507.1	7.9
		+			510.2	11.0
			–		510.6	11.4
				–	510.7	11.5
		+		–	511.0	11.8
			–	–	511.4	12.2
		+	–		511.7	12.5
		+	–	–	512.5	13.3



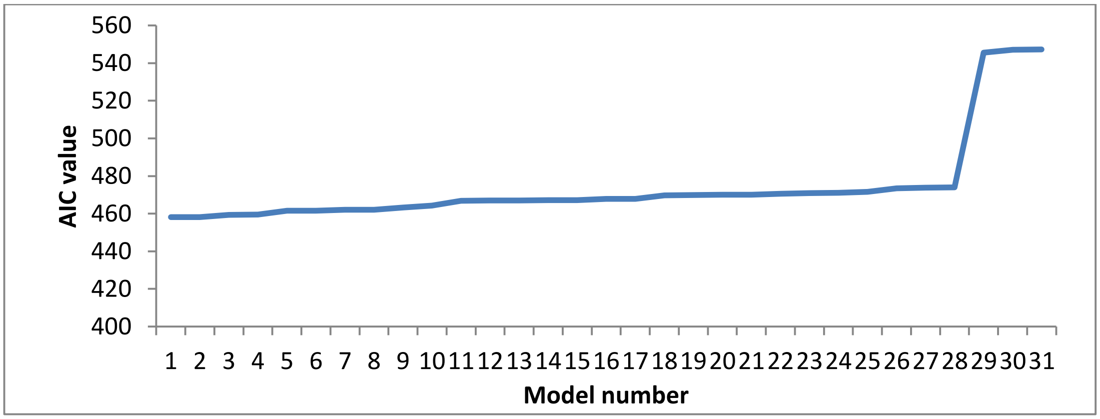
5. Yellow-breasted Fruit-dove *Ptilinopus occipitalis*

Factor 2	AvGirth	AvPath	Factor 1	Factor 3	AIC	ΔAIC
+**					742.4	0
+**	+				742.6	0.2
+**		+			743.0	0.6
+**	+	+			743.1	0.7
+*		+	+		743.3	0.9
+**			+		743.4	1.0
+*	+	+	+		743.4	1.0
+**	+		+		743.5	1.1
+**				+	743.7	1.3
+**	+			+	743.7	1.3
+**	+	+		+	744.2	1.8
+**		+		+	744.3	1.9
+*	+	+	+	+	744.8	2.4
+**			+	+	744.9	2.5
+**	+		+	+	744.9	2.5
+*		+	+	+	744.9	2.5
	+				747.7	5.3
		+			747.8	5.4
		+	+		747.8	5.4
	+	+	+		747.9	5.5
	+	+			748.0	5.6
			+		748.3	5.9
	+		+		748.5	6.1
				+	748.6	6.2
	+			+	748.7	6.3
		+		+	749.0	6.6
	+	+		+	749.0	6.6
		+	+	+	749.4	7.0
	+	+	+	+	749.4	7.0
			+	+	749.7	7.3
	+		+	+	749.8	7.4



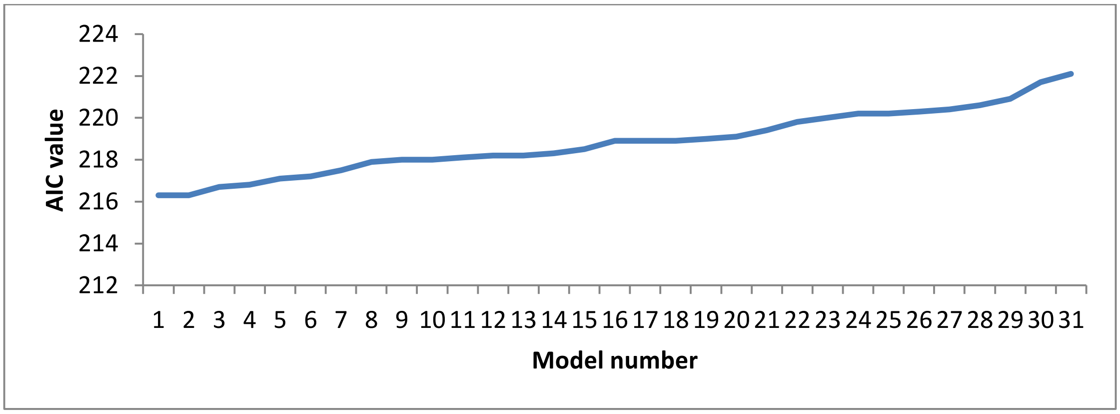
6. Black-chinned Fruit-dove *Ptilinopus leclancheri*

AveAlt	AvGirth	Factor 1	AvSlope	Factor 2	AIC	ΔAIC
–**	+**	+*			458.1	0.0
–**	+**	+*	–		458.2	0.1
–**	+**	+*		–	459.4	1.3
–**	+**	+*	–	–	459.5	1.4
–**	+**				461.5	3.4
–**	+**		–		461.6	3.5
–**	+**			–	462.0	3.9
–**	+**		–	–	462.0	3.9
–**	+*		–		463.2	5.1
–**		+*	–	–	464.3	6.2
–**			–		466.9	8.8
–**					467.0	8.9
	+*	+*	–		467.0	8.9
	+*	+*			467.1	9.0
–**			–	–	467.2	9.1
+*		+*	–	–	467.8	9.7
+*		+*		–	467.9	9.8
	+*		–	–	469.8	11.7
	+*		–		469.9	11.8
	+*			–	470.0	11.9
	+*				470.1	12.0
		+*	–		470.5	12.4
		+*			470.9	12.8
		+*	–	–	471.1	13.0
		+*		–	471.6	13.5
			–	–	473.4	15.3
			–		473.8	15.7
				–	473.9	15.8
–				–	545.6	87.5
–		+		–	547.1	89.0
–		+			547.3	89.2



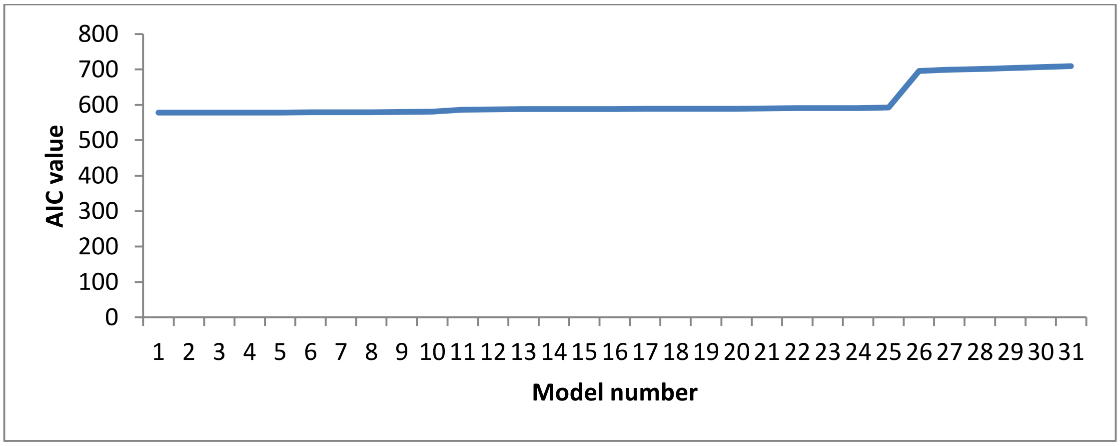
7. Green Imperial-pigeon *Ducula aenea*

AvGirth	AvAlt	CCover	AvPath	AvSlope	AIC	ΔAIC
+	–			–	216.3	0
+				–	216.3	0
+		+		–	216.7	0.4
+	–	+		–	216.8	0.5
+			–	–	217.1	0.8
+	–		–	–	217.2	0.9
				–	217.5	1.2
	–			–	217.9	1.6
		+		–	218	1.7
+		+	–	–	218	1.7
+	–				218.1	1.8
+					218.2	1.9
+	–	+	–	–	218.2	1.9
			–	–	218.3	2
	–	+		–	218.5	2.2
	–		–	–	218.9	2.6
+		+			218.9	2.6
+	–	+			218.9	2.6
+			–		219	2.7
+	–		–		219.1	2.8
		+	–	–	219.4	3.1
	–				219.8	3.5
	–	+	–	–	220	3.7
+		+	–		220.2	3.9
		+			220.2	3.9
+	–	+	–		220.3	4
			–		220.4	4.1
	–	+			220.6	4.3
	–		–		220.9	4.6
		+	–		221.7	5.4
	–	+	–		222.1	5.8



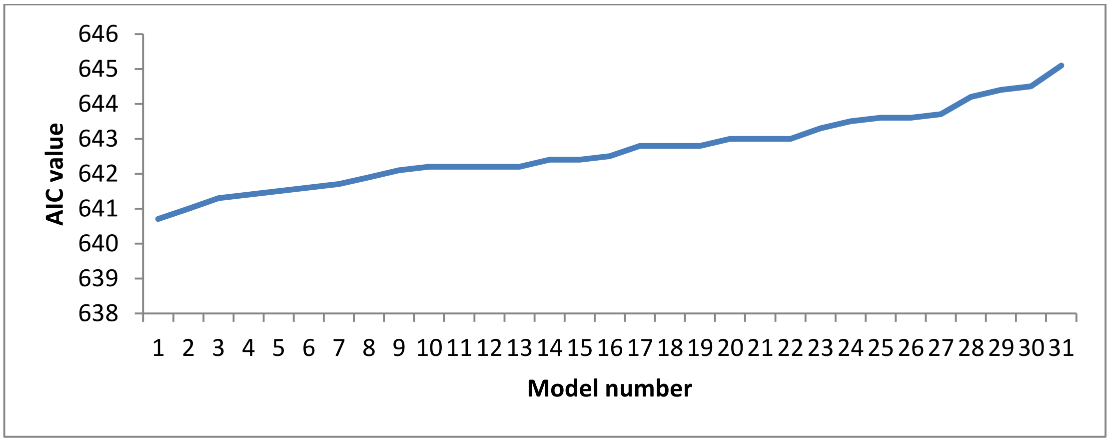
8. Philippine Cuckoo-dove *Macropygia tenuirostris*

AvAlt	AvPath	AvGirth	AvSlope	Factor 3	AIC	ΔAIC
+***	–	+	–		577.8	0
+***		+	–		578	0.2
+***	–		–		578.3	0.5
+***					578.4	0.6
+***			–		578.6	0.8
+***	–	+		+	578.9	1.1
+***	–	+	–	+	579.3	1.5
+***		+*	–	+	579.5	1.7
+***				+	580	2.2
+***	–		–	+	580.5	2.7
	–	+			586.4	8.6
	–	+		+	587.4	9.6
		+*			587.7	9.9
	–	+	–		587.7	9.9
	–				588	10.2
	–	+*	–	+	588.6	10.8
		+*	–		588.7	10.9
		+*		+	588.8	11
	–			+	589.2	11.4
	–		–		589.4	11.6
		+*	–	+	589.9	12.1
			–		590.7	12.9
				+	590.9	13.1
	–		–	+	591	13.2
			–	+	592.6	14.8
+***			– ***	–	696	118.2
+***	– **	+*			699.1	121.3
+***	– **				701.5	123.7
+***	– **			–	703.5	125.7
+***		+**			706.9	129.1
+***		+**		–	708.9	131.1

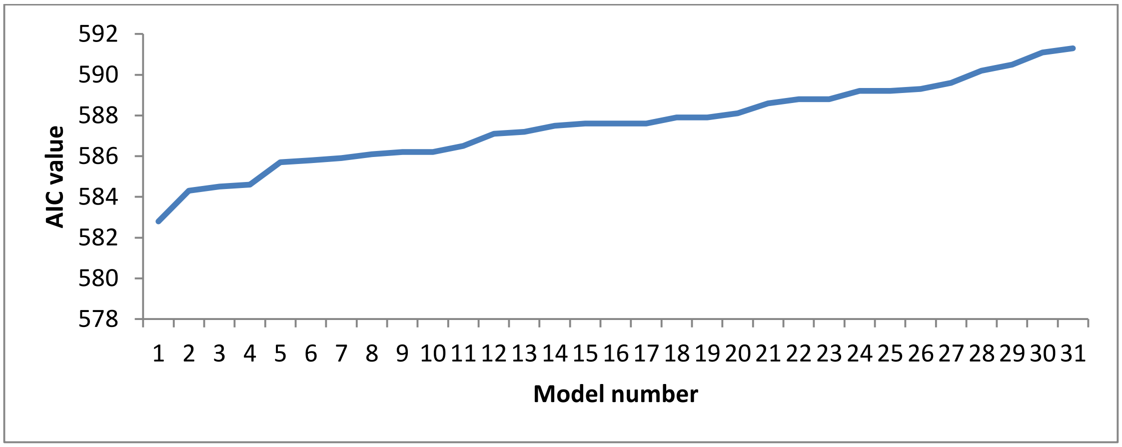


10. Common Emerald Dove *Chalcophaps indica*

Factor 2	AvAlt	AvPath	CCover	Factor 1	AIC	ΔAIC
	–				640.7	0.0
	–			–	641.0	0.3
–	–				641.3	0.6
–			+		641.4	0.7
	–	–			641.5	0.8
				–	641.6	0.9
–	–			–	641.7	1.0
	–	–		–	641.9	1.2
–					642.1	1.4
–				–	642.2	1.5
–	–	–			642.2	1.5
–	–		+		642.2	1.5
–			+	–	642.2	1.5
		–			642.4	1.7
			+		642.4	1.7
		–		–	642.5	1.8
			+	–	642.8	2.1
	–	–	+		642.8	2.1
–	–	–		–	642.8	2.1
–		–			643.0	2.3
–			+		643.0	2.3
–	–		+	–	643.0	2.3
–		–		–	643.3	2.6
	–	–	+	–	643.5	2.8
–			+	–	643.6	2.9
–	–	–	+		643.6	2.9
		–	+		643.7	3.0
		–	+	–	644.2	3.5
–	–	–	+	–	644.4	3.7
–		–	+		644.5	3.8
–	–		+	–	645.1	4.4

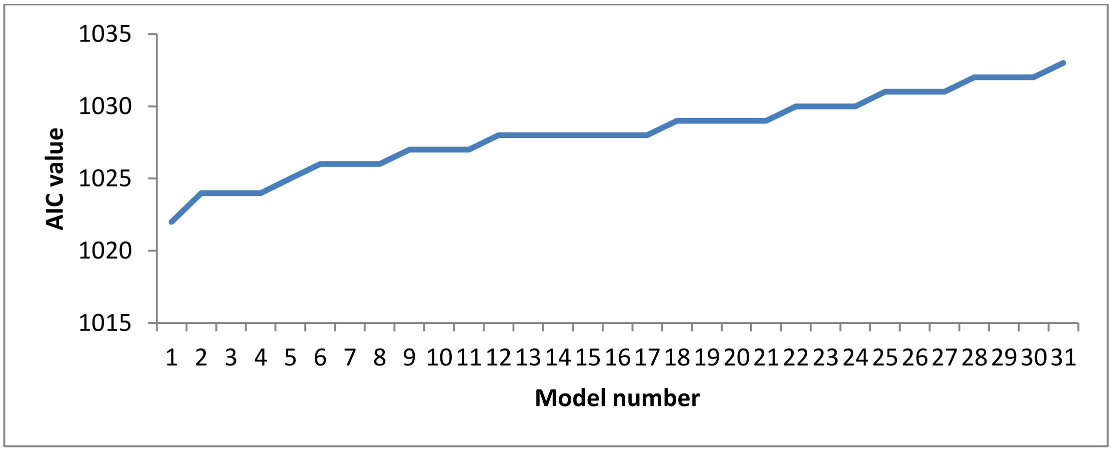


AvGirth	Factor 1	Factor 3	AvPath	CCover	AIC	ΔAIC
+	+*	– *			582.8	0.0
+	+*	– *	–		584.3	1.5
	+*	– *			584.5	1.7
+	+	– *		+	584.6	1.8
+*	+				585.7	2.9
+*		–		+	585.8	3.0
	+*	– *	–		585.9	3.1
	+*	– *		+	586.1	3.3
+*		–			586.2	3.4
+	+	– *	–	+	586.2	3.4
+*		–	–		586.5	3.7
+*		–	–	+	587.1	4.3
+*	+		–		587.2	4.4
+*					587.5	4.7
+*	+			+	587.6	4.8
	+	– *	–	+	587.6	4.8
		–		+	587.6	4.8
	+*				587.9	5.1
+*				+	587.9	5.1
+*			–		588.1	5.3
		–	–		588.6	5.8
		–			588.8	6.0
		–	–	+	588.8	6.0
	+		–		589.2	6.4
+*	+		–	+	589.2	6.4
+*			–	+	589.3	6.5
	+			+	589.6	6.8
				+	590.2	7.4
			–		590.5	7.7
	+		–	+	591.1	8.3
			–	+	591.3	8.5



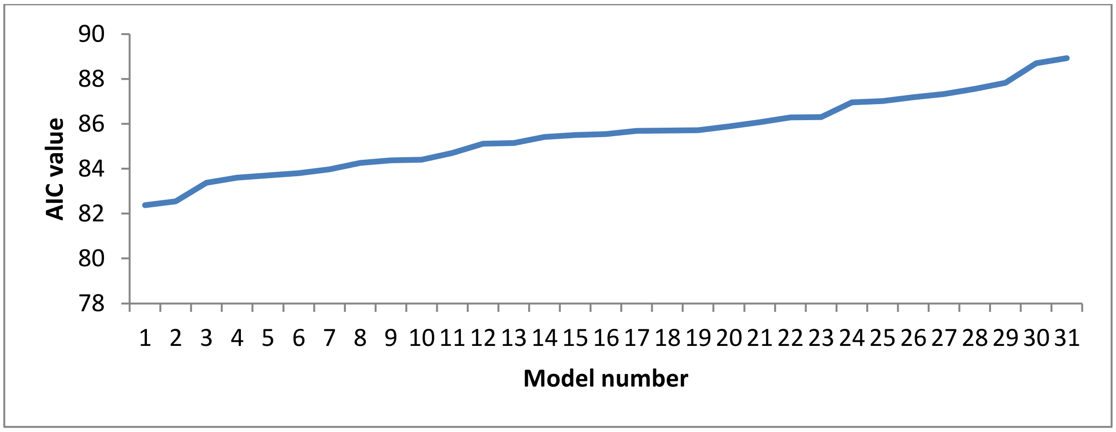
12. Guaiabero *Bolbopsittacus lunulatus*

Factor 1	Factor 3	AvGirth	CCover	Factor 2	AIC	ΔAIC
+*				– *	1022	0
+*	+			– *	1024	2
+*		+		– *	1024	2
+*			+	– *	1024	2
+*	+	+		– *	1025	3
				– *	1026	4
+*	+		+	– *	1026	4
+*		+	+	– *	1026	4
+*					1027	5
			+	– *	1027	5
+*	+	+	+	– *	1027	5
+*	+				1028	6
+*		+			1028	6
	+			– *	1028	6
		+		– *	1028	6
	+		+	– *	1028	6
		+	+	– *	1028	6
+			+		1029	7
+*	+	+			1029	7
	+	+		– *	1029	7
	+	+	+	– *	1029	7
			+		1030	8
+	+		+		1030	8
+*		+	+		1030	8
	+				1031	9
		+			1031	9
+	+	+	+		1031	9
	+	+			1032	10
	+		+		1032	10
		+	+		1032	10
	+	+	+		1033	11



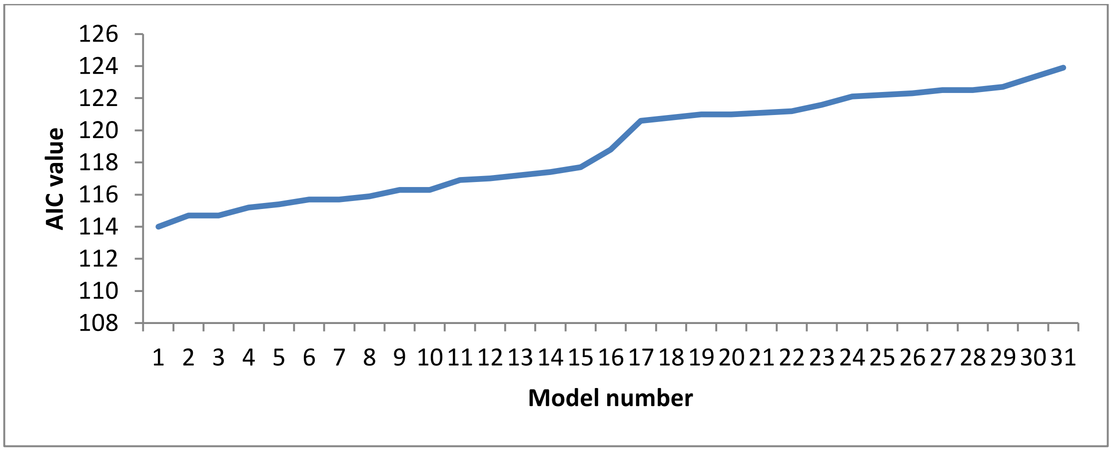
13. Blue-naped Parrot *Tanygnathus lucionensis*

Factor 1	Factor 3	AvGirth	AvSlope	Factor 2	AIC	ΔAIC
				–	82.37	0.00
	–			–	82.55	0.18
–	–			–	83.38	1.01
–				–	83.60	1.23
		+		–	83.70	1.33
	–	+		–	83.80	1.43
			–	–	83.97	1.60
–	–	+		–	84.26	1.89
	–				84.38	2.01
	–		–	–	84.40	2.03
–		+		–	84.70	2.33
–			–	–	85.12	2.75
–	–		–	–	85.15	2.78
		+	–	–	85.42	3.05
–					85.50	3.13
		+			85.54	3.17
–	–				85.68	3.31
			–		85.70	3.33
	–	+	–	–	85.71	3.34
	–	+			85.89	3.52
–	–	+	–	–	86.07	3.70
	–		–		86.28	3.91
–		+	–	–	86.30	3.93
–		+			86.95	4.58
–	–	+			87.02	4.65
–			–		87.18	4.81
		+	–		87.33	4.96
–	–		–		87.55	5.18
	–	+	–		87.83	5.46
–		+	–		88.70	6.33
–	–	+	–		88.93	6.56



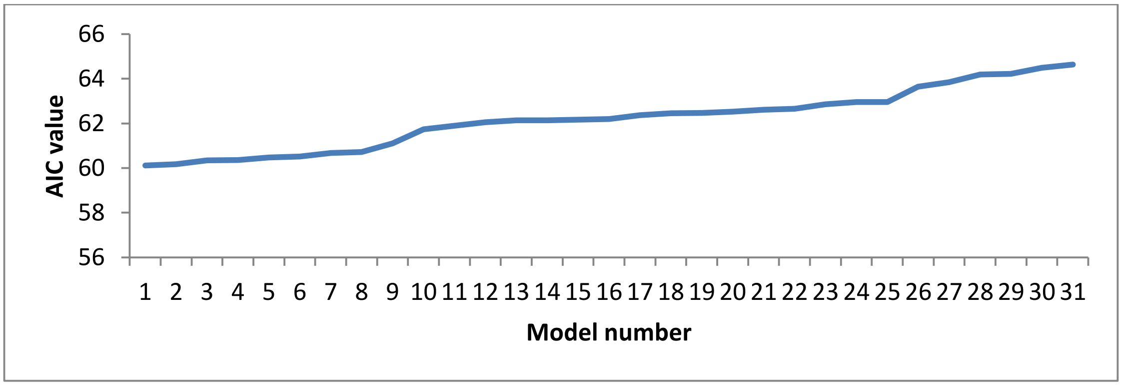
14. Green Racquet-tail *Prioniturus luconensis*

Factor 1	Factor 2	AvAlt	AvSlope	CCover	AIC	ΔAIC
		– *			114.0	0.0
+		– *			114.7	0.7
+		– *		–	114.7	0.7
+	–	– *		–	115.2	1.2
	–	– *			115.4	1.4
		– *	+		115.7	1.7
		– *		–	115.7	1.7
+	–	– *			115.9	1.9
+		– *	+		116.3	2.3
+		– *	+	–	116.3	2.3
+	–	– *	+	–	116.9	2.9
	–	– *		–	117.0	3.0
	–	– *	+		117.2	3.2
		– *	+	–	117.4	3.4
+	–	– *	+		117.7	3.7
	–	– *	+	–	118.8	4.8
+					120.6	6.6
	–				120.8	6.8
+				–	121.0	7.0
+	–			–	121.0	7.0
			+		121.1	7.1
				–	121.2	7.2
+	–				121.6	7.6
+			+		122.1	8.1
	–			–	122.2	8.2
+			+	–	122.3	8.3
	–		+		122.5	8.5
+	–		+	–	122.5	8.5
			+	–	122.7	8.7
+	–		+		123.3	9.3
	–		+	–	123.9	9.9



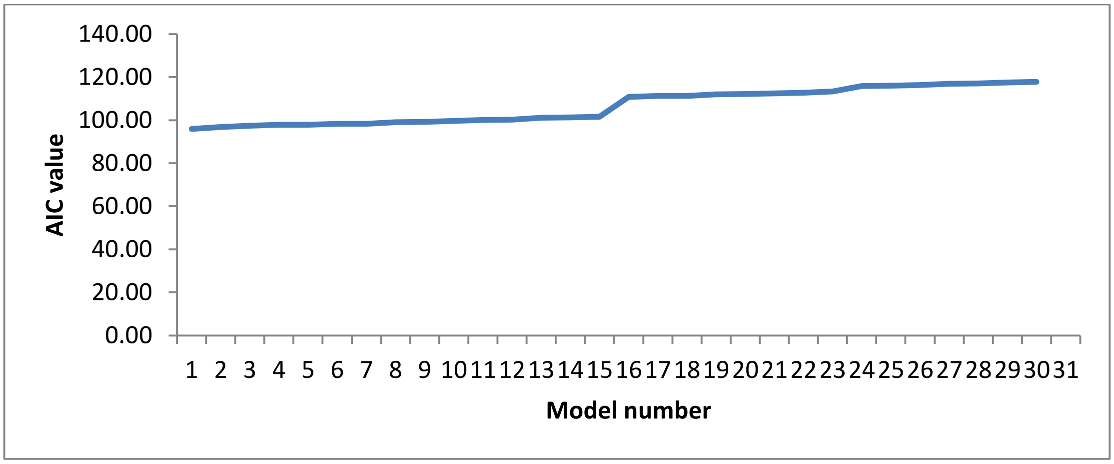
15. Blue-crowned Racquet-tail *Prioniturus discurus*

Factor 1	Factor 2	AvAlt	AvPath	CCover	AIC	ΔAIC
–		–	+		57.26	0.00
		–	+*		57.34	0.08
–	–	–	+		57.68	0.42
	–	–	+		57.85	0.59
–		–	+	+	57.98	0.72
–	–	–	+	+	58.57	1.31
–	–	–			58.58	1.32
–		–			58.65	1.39
		–	+	+	59.34	2.08
		–			59.76	2.5
	–	–	+	–	59.84	2.58
			+		60.12	2.86
	–		+		60.17	2.91
	–	–			60.20	2.94
–			+		60.35	3.09
–			+	+	60.36	3.10
–	–				60.48	3.22
–	–		+		60.51	3.25
–	–	–		+	60.54	3.28
–		–		+	60.60	3.34
–					60.68	3.42
–	–		+	+	60.72	3.46
		–		–	60.88	3.62
	–	–		–	60.97	3.71
	–				61.10	3.84
			+	+	62.05	4.79
	–		+	+	62.14	4.88
–	–			+	62.20	4.94
–				+	62.37	5.11
	–			–	62.61	5.35
				–	62.86	5.60



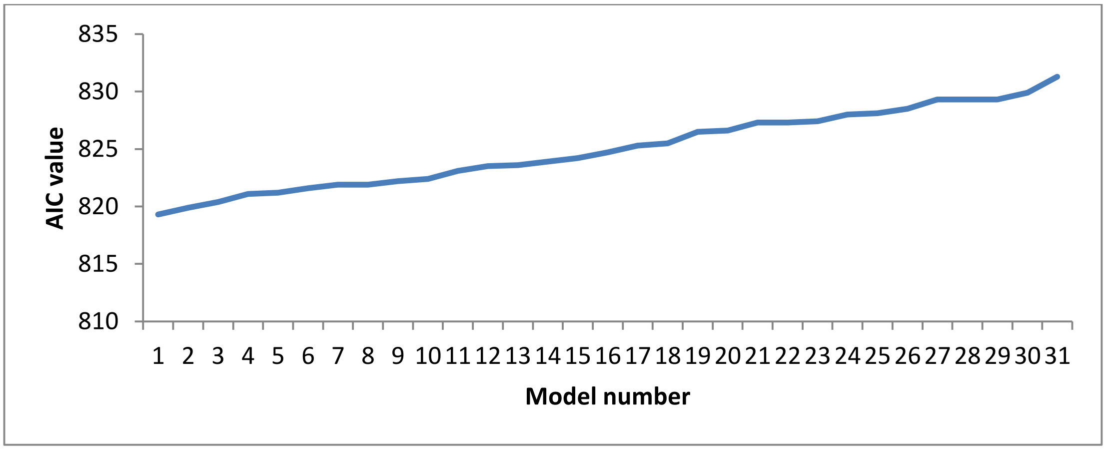
16. Luzon Racquet-tail *Prioniturus montanus*

AvPath	AvAlt	Factor 1	Factor 2	Factor 3	AIC	ΔAIC
–	+***	–		–	94.79	0
–	+***			–	95.92	1.13
–	+***	–	+	–	96.77	1.98
–	+***		+	–	97.47	2.68
–	+***				97.81	3.02
	+***	–		–	97.89	3.1
–	+***		+		98.28	3.49
–	+***	–			98.32	3.53
	+***			–	99.06	4.27
–	+***	–	+		99.21	4.42
	+***	+	+	–	99.65	4.86
	+***		+	–	100.10	5.31
	+***		+		100.20	5.41
	+***	+			101.10	6.31
	+***	+	+		101.30	6.51
	+***				101.50	6.71
–		+		–	110.80	16.01
–					111.20	16.41
–		+			111.20	16.41
–				–	112.00	17.21
–			+		112.10	17.31
–		+	+		112.50	17.71
–		+	+	–	112.70	17.91
–			+	–	113.40	18.61
		+		–	115.90	21.11
		+			116.00	21.21
			–		116.30	21.51
		+	–		116.90	22.11
				–	117.00	22.21
		+	–	–	117.50	22.71
			–	–	117.80	23.01



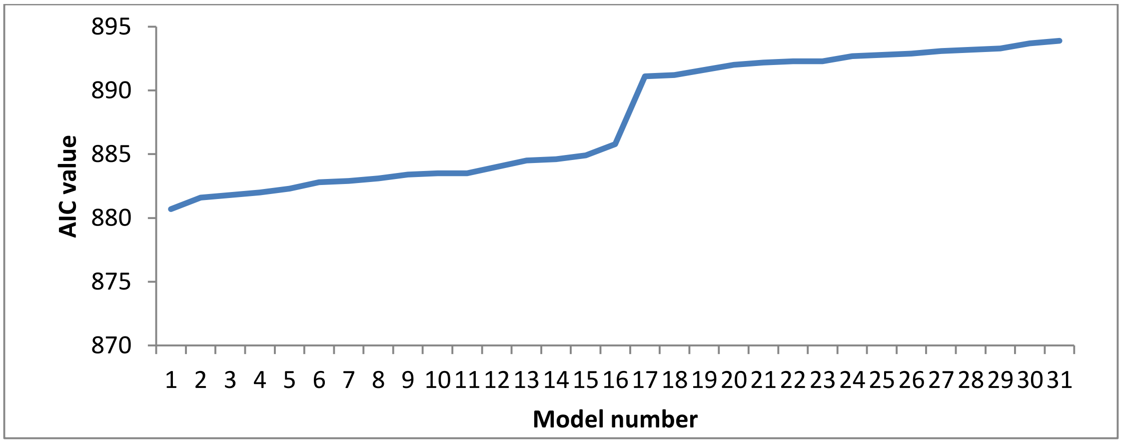
17. Colasisi *Loriculus philippensis*

Factor 1	AvSlope	AvGirth	Factor 2	Factor 3	AIC	ΔAIC
+	– **				819.3	0
+	– **			–	819.9	0.6
	– **				820.4	1.1
+	– **		+		821.1	1.8
+	– **	+			821.2	1.9
	– **			–	821.6	2.3
+	– **	+		–	821.9	2.6
+	– **		+	–	821.9	2.6
	– **		+		822.2	2.9
	– **	+			822.4	3.1
+	– **	+	+		823.1	3.8
	– **		+	–	823.5	4.2
	– **	+		–	823.6	4.3
+	– **	+	+	–	823.9	4.6
	– **	+	+		824.2	4.9
+					824.7	5.4
+*				–	825.3	6
	– **	+	+	–	825.5	6.2
+			+		826.5	7.2
+		+			826.6	7.3
+*		+		–	827.3	8
+*			+	–	827.3	8
				– **	827.4	8.1
			+		828	8.7
		+			828.1	8.8
+		+	+		828.5	9.2
		+		–	829.3	10
			+	–	829.3	10
+*		+	+	–	829.3	10
		+	+		829.9	10.6
		+	+	–	831.3	12



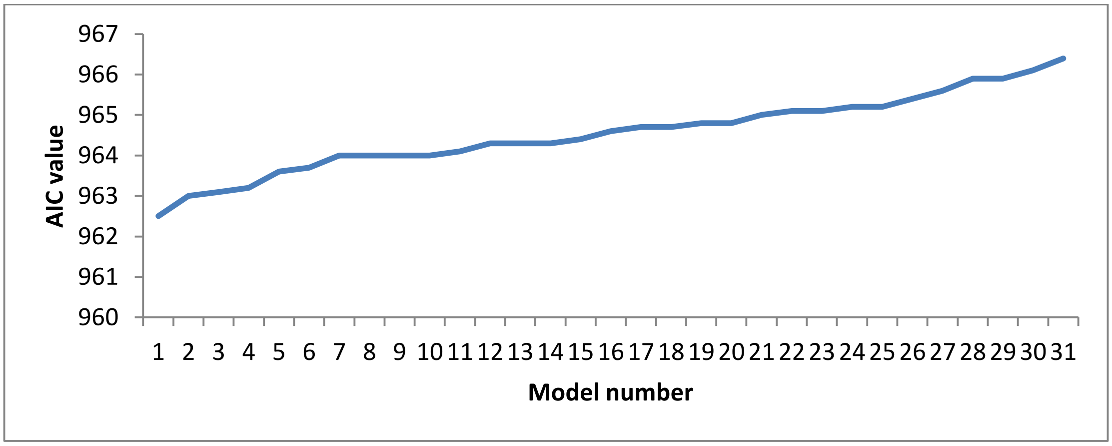
18. Luzon Tarictic *Penelopides manillae*

AvSlope	AvPath	Factor 2	Factor 3	AvAlt	AIC	ΔAIC
– *	–		+	– ***	880.7	0
– *			+	– ***	881.6	0.9
– *	–	+	+	– ***	881.8	1.1
– *	–			– ***	882	1.3
	–		+	– ***	882.3	1.6
– *				– ***	882.8	2.1
– *		+	+	– ***	882.9	2.2
– *	–	+		– ***	883.1	2.4
	–			– ***	883.4	2.7
			+	– ***	883.5	2.8
	–	+	+	– ***	883.5	2.8
– *		+		– ***	884	3.3
				– ***	884.5	3.8
	–	+		– ***	884.6	3.9
		+	+	– ***	884.9	4.2
		+		– ***	885.8	5.1
				+	891.1	10.4
–				+	891.2	10.5
–	–			+	891.6	10.9
–		+	+		892	11.3
	–			+	892.2	11.5
–					892.3	11.6
–	–	+	+		892.3	11.6
–	–				892.7	12
		+	+		892.8	12.1
	–	+	+		892.9	12.2
–		+			893.1	12.4
	–				893.2	12.5
–	–	+			893.3	12.6
		+			893.7	13
	–	+			893.9	13.2



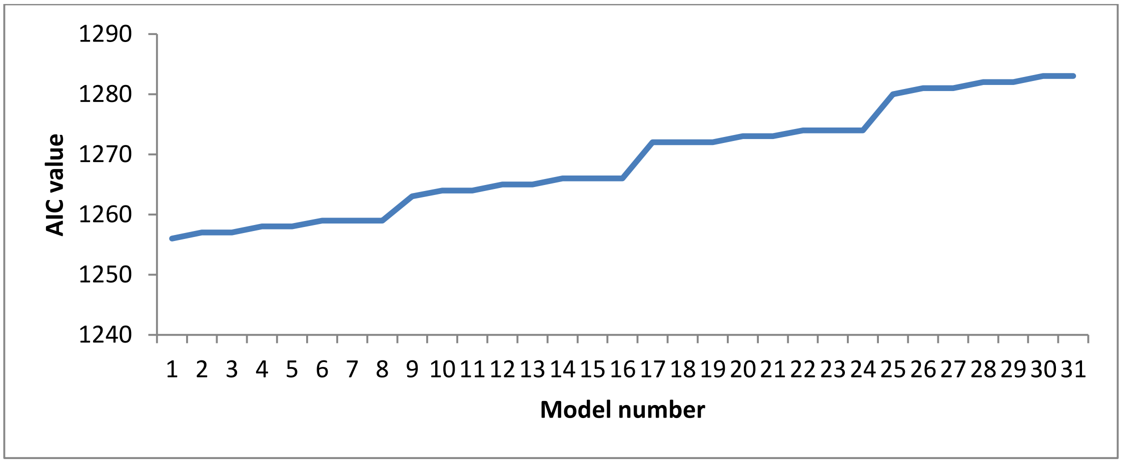
19. Rufous Hornbill *Buceros hydrocorax*

Factor 1	Factor 2	AvAlt	AvGirth	Factor 3	AIC	ΔAIC
				–	962.5	0
			+	–	963	0.5
	–			–	963.1	0.6
		+		–	963.2	0.7
–				–	963.6	1.1
	–		+	–	963.7	1.2
			+		964	1.5
–			+	–	964	1.5
	–	+		–	964	1.5
		+	+	–	964	1.5
–					964.1	1.6
	–				964.3	1.8
–			+		964.3	1.8
–	–			–	964.3	1.8
–		+		–	964.4	1.9
		+			964.6	2.1
	–		+		964.7	2.2
–	–		+	–	964.7	2.2
–	–				964.8	2.3
	–	+	+	–	964.8	2.3
–	+	+		–	965	2.5
–		+			965.1	2.6
–	–		+		965.1	2.6
		+	+		965.2	2.7
–	–	+		–	965.2	2.7
	–	+			965.4	2.9
–		+	+		965.6	3.1
–	–	+			965.9	3.4
–	–	+	+	–	965.9	3.4
	–	+	+		966.1	3.6
–	–	+	+		966.4	3.9



19. Species richness

Factor 2	AvGirth	AvSlope	Factor 1	Factor 3	AIC	ΔAIC
+	+***	–**			1256	0
	+***	–**			1257	1
+	+***	–**	+		1257	1
	+***	–**	+		1258	2
+	+***	–**		+	1258	2
	+***	–**		+	1259	3
	+***	–**	+	+	1259	3
+	+***	–**	+	+	1259	3
+	+***				1263	7
	+***				1264	8
+	+***		+		1264	8
	+***		+		1265	9
+	+***			+	1265	9
	+***			+	1266	10
	+***		+	+	1266	10
+	+***		+	+	1266	10
		–**			1272	16
+		–**			1272	16
		–**	+		1272	16
		–**		+	1273	17
+		–**	+		1273	17
+		–**		+	1274	18
		–**	+	+	1274	18
+		–**	+	+	1274	18
+					1280	24
			+		1281	25
+			+		1281	25
				+	1282	26
+				+	1282	26
			+	+	1283	27
+			+	+	1283	27



Appendix 5.1 Frugivore encounters and numbers encountered (in parentheses) per path type during the second field season in Bataan Natural Park from December 2011 to March 2012.

Species	Bird encounters (individuals encountered) per path type		
	Random paths Effort = 102.8 km	Hunter/farmer trails Effort = 147.2 km	Access roads Effort = 90 km
Treron pompadora	21 (25)	18 (45)	10 (25)
Phapitreron leucotis	481 (496)	437 (465)	312 (330)
Phapitreron amethystinus	187 (189)	136 (140)	56 (59)
Ptilinopus merrilli	1 (1)	0	1 (1)
Ptilinopus occipitalis	147 (163)	134 (157)	24 (25)
Ptilinopus leclancheri	9 (9)	12 (23)	10 (11)
Ducula carola	0	0	1 (1)
Ducula aenea	36 (93)	35 (60)	16 (56)
Macropygia tenuirostris	41 (46)	35 (37)	7 (9)
Chalcophaps indica	31 (33)	59 (64)	30 (30)
Gallicolumba luzonica	2 (2)	12 (13)	0
Bolbopsittacus lunulatus	238 (310)	361 (453)	260 (316)
Tanygnathus lucionensis	6 (9)	2 (3)	3 (3)
Prioniturus luconensis	21 (44)	26 (39)	6 (8)
Loriculus philippensis	112 (143)	124 (150)	50 (77)
Penelopides manillae	90 (135)	106 (186)	66 (88)
Buceros hydrocorax	12 (31)	11 (39)	5 (7)