ASSESSING DISTRIBUTION, ABUNDANCE AND IMPACTS OF TRADE AND HABITAT CHANGE IN WESTERN POPULATIONS OF AFRICAN GREY PARROT (PSITTACUS ERITHACUS)

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Abstract

In Ghana, many large avian frugivores face very serious threats, including habitat loss, hunting, and capture for the pet trade. However, basic ecological information is lacking for most species including the heavily-traded Grey Parrot *Psittacus erithacus*. The aim of my PhD was therefore to investigate the current distribution, abundance and ecology of Grey Parrot and other large frugivores to help inform their future conservation.

I conducted surveys for twenty species of pigeons, parrots, turacos and hornbills in forty-two 10 km × 10 km survey squares in southwest Ghana. Only two species, West African Pied Hornbill *Lophoceros semifasciatus* and African Green Pigeon *Treron calvus*, were recorded in most survey squares. The most restricted and rare species included large-bodied species such as Great Blue Turaco *Corythaeola cristata*, Yellow-casqued Hornbill *Ceratogymna elata* and Black-casqued Hornbill *C. atrata*. Canonical Correspondence Analysis showed that large hornbills were especially restricted to large forest reserves with low anthropogenic disturbance. I then used Maxent to predict more precisely the distribution of the frugivores across Ghana, and identify their responses to predictors such as land cover types, enhanced vegetation index (EVI), human population density, and climate data. Frugivores showed varying associations with Ghana's large forest reserves, with Afep Pigeon *Columba unicincta*, Great Blue Turaco, and Black Dwarf Hornbill *Tockus hartlaubi* among the most restricted. Most species had highest occurrence probabilities in the southwest of the country. The main driver of distributions was land cover type, with forest habitats preferred in 90% of species. Differences in human population density and EVI were seldom important. The large southwestern forest reserves are key sites for Ghana's frugivores, and it is crucial that they are adequately protected and managed.

Grey Parrot is believed to have undergone rapid population decline, yet there are almost no quantitative data properly supporting this from anywhere within its huge range. I reviewed its historical abundance across Ghana, undertook targeted searches across the country's forest zone, repeated counts at 22 parrot roosts first performed two decades ago and gauged around 900 people's perceptions of the decline and its causes. In over 150 days of fieldwork, just 32 groups were recorded. Encounter rates were 15 times lower than those from the early 1990s. No active roosts, i.e. roosts in current use, were found, and just a handful of birds seen near three roosts that each harboured 700–1200 birds two decades ago. Interviewees stressed the importance of very tall trees of commercially important timber species for nesting and roosting. Ghana has lost 90–99% of its Grey Parrots since 1992, and there is no evidence that, away from one or two localities, declines are less severe anywhere else in West Africa. Despite declines, Grey Parrots paradoxically remain reasonably widely distributed. I developed multiple historical and current Maxent models for the species based on various presence data sources: field surveys from the early 1990s and 2012–14, records from the Global Biodiversity Information Facility, and interview data. Models of historical distribution showed high suitability over much of the study area. Current distributions were predicted to be much more patchy, with large areas unsuitable, but with high suitability in the extreme south/southwest. Historically, Grey Parrot distribution was correlated most strongly with high rainfall, while current distribution is more closely linked with land use.

Levels of exploitation of Grey Parrots have been unsustainable and regulation of the trade through quota schemes and enforcement of trade embargoes needs to be strengthened. Ghana should also reintroduce shade cocoa agriculture to improve habitat quality for the Grey Parrot and other frugivores.

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Chapter 1

THE GREY PARROT: AN INTRODUCTORY SYNTHESIS ON BIOLOGY, ANTHROPOGENIC STRESSORS AND CONSERVATION ISSUES

1.1 The extinction crisis and the role of wildlife trade

The subject of global biodiversity decline has been to the fore for a long time (e.g. Wilson 1988, Pimm 1995, Jenkins 2003), and there is evident consensus within the international community that modern rates of extinction and endangerment have reached crisis level (Stork 2010). This is considered the planet's 'sixth extinction crisis' although the first to be caused by human beings, with estimates of seven times more than what is reported by the IUCN (Régnier et al. 2015, McCallum 2015). It has even been suggested that current rates of extinction could be as many as a thousand times greater than natural background rates (Pimm 1995).

Researching the phenomenon of extinction is vital to biodiversity conservation, and a clear knowledge of trends in the taxonomic and geographic patterns and causes of extinction may improve the chances of curtailing the rate of future human-induced extinctions (Szabo et al. 2012). The majority of species threatened with extinction occur in 'biodiversity hotspots' mainly in the tropics, including the Guinean forests of Sub-Saharan Africa, the Tropical Andes and the Atlantic Forests in Central and South America, and many areas in Southeast Asia (e.g. Mittermeier et al. 2011). The main drivers of these extinctions include overexploitation of wild populations for trade, habitat loss through the expansion of agriculture, urbanization and industrial development, and invasive species in ecosystems (Vitousek et al. 1997, Millennium Ecosystem Assessment 2005, Wake and Vredenburg 2008).

The trade in wildlife involves hundreds of millions of individual plants and animals taken from tens of thousands of species (Collen et al. 2013). Global legal wildlife trade was estimated to be worth some \$300 billion in 2005, whereas the illegal wildlife trade alone, excluding timber and fisheries, is worth \$7.8–10 billion annually (Roe 2008, TRAFFIC: http://www.traffic.org/trade/). A small polished elephant tusk, for example, could sell for \$35,000 on the Chinese market (Rice 2014).

About one third of all extant bird species have been traded across international borders, mainly for pet keeping, but many of these species are also used for other purposes such as food, medicine, sport hunting and clothing (BirdLife International 2008d). The international pet trade is a major contributory factor to the threat status of many of the world's bird species (Butchart 2008). Probably more than 145 bird species have become extinct since the year 1500, with a further 19 lost in the last quarter of the 20th century, while three more are thought to have gone extinct since 2000 (Butchart et al. 2006a, BirdLife International 2014), including Spix's Macaw *Cyanopsitta spixii* (Critically Endangered: Possibly Extinct in the Wild), the last known free-living individual of which had vanished in Brazil by the end of 2000.

Bird extinctions, however, could have dire consequences for biodiversity in general, owing to the importance of birds in ecological processes (Sekercioglu 2006, Whelan et al. 2015). Frugivores, especially, perform vital ecosystem services that include the maintenance of forest structure (Cordeiro and Howe 2001, Sodhi et al. 2008). Some conservation efforts to prevent avian extinctions have been rewarded, involving an estimated 16 bird species that would have become extinct between 1994 and 2004 in the absence of conservation programmes that managed their threats, reduced rates of population decline and/or increased population sizes (Butchart et al. 2006b). In addition, during this 10-year period, 49 Critically Endangered species (28%

of the total) are thought to have benefited from conservation action such that their rate of decline was less severe (24 species), or improved in status (25 species) (BirdLife International 2008a). Classic examples of the achievements resulting from such active conservation efforts are three Mascarene endemic species rescued from the brink of extinction, namely Mauritius Kestrel *Falco punctatus*, Pink Pigeon *Nesoenas mayeri* and Mauritius Parakeet *Psittacula eques* (Jones and Swinnerton 1997). Regrettably, however, such conservation efforts are in a minority, and certain groups of birds, most notably parrots, remain disproportionately at risk (Bennett and Owens 1997).

1.2 Challenges in the conservation of the world's parrots

1.2.1 Why are parrots so severely threatened?

Parrots form an assemblage of some 350 species that occur globally, but with strongholds in tropical and subtropical regions, mainly South America (123 species), Central America/Caribbean (54 species), Australasia (108 species) and Asia (99 species) (Juniper and Parr 1998). Parrot species richness in mainland Africa (21 species), however, is relatively low (Marsden and Royle 2015). Owing to their brilliant colours, strong 'personalities' and ability to talk, parrots have very high popular appeal among the public, especially as pets (Collar 1997), but although they have been well studied by ethologists, typically very little is known about their ecology in the wild (Collar 1998, Juniper and Parr 1998).

A myriad of causal factors act in synergy to cause declines in the populations of many species of parrot and place them at risk of extinction. Many species occur at naturally low population densities even in undisturbed habitats. Species belonging to the genera *Tanygnathus*, *Aratinga* and *Ara* are typical examples (Marsden and Royle 2015). Some parrot species have also become restricted by widespread habitat destruction to small fragments of their original habitat (Juniper and Parr 1998). Many parrots also tend to be K-selected (e.g. Pianka 1970), characterised by large body size, long lifespan, low productivity, extended parental care and slow rates of recruitment. Parrots also normally have colourful and attractive plumage (Collar 1997), and possess extraordinary abilities for mimicking human speech and other sounds, as well as exceptional cognitive abilities (Pepperberg 1994, 2006). They are therefore some of the most sought-after animals as pets (Tella and Hiraldo 2014).

The high demand for parrots for both the international and progressively burgeoning domestic markets (Pires 2012) is a major factor contributing to the severity of their threat status. The trade is extensive, and it has been estimated that some one million parrots were traded in the three years 1998–2000 (Gastañaga et al. 2011). Many species are particularly targeted by trade, but the Grey Parrot *Psittacus erithacus* is the species with by far the highest trade figures (Marsden and Royle 2015).

Habitat loss and reduction in habitat quality—especially in terms of the removal of large trees through selective logging and other degrading land-use activities—are the other important factors in parrot population declines (e.g. Collar 1997, Juniper and Parr 1998, Manning et al. 2013), as parrots typically nest in very large trees (e.g. Marsden and Jones 1997, Monterrubio-Rico and Enkerlin-Hoeflich 2004). Consequently, towards the end of the 20th century, the vast majority (93%) of threatened parrots were forest species (Collar 2000). Many species exhibit specific habitat requirements, with Eclectus Parrots *Eclectus roratus*, for example, having particular needs in respect of tree species, hollow height above ground, aperture orientation, and internal depth (Heinsohn et al. 1997, Legge et al. 2004). Habitat degradation may result in the loss of both nest sites and food sources, but also in direct disturbance to parrot species (Juniper and Parr 1998).

1.2.2 Parrots and the international pet trade

The overexploitation of wildlife is one of the main causes of biodiversity loss globally (Wilcove et al. 1998, Blundell and Mascia 2005), and the targeted exploitation of species for international trade, together with other confounding factors including habitat loss, pose a significant threat (Pain et al. 2006, CITES 2013b). Hundreds of millions of plants and animals are traded globally, with estimated annual gains of billions of dollars from legal transactions (St John et al. 2012, CITES 2013b). This legal trade represents only a fraction of the whole, but the illegal trade cannot be quantified with any certainty owing to its clandestine nature (Karesh et al. 2005, Rosen and Smith 2010). Moreover, the combination of unreported domestic trade and high pre-export mortality for many species of wildlife strongly suggests that documented levels of extraction of wildlife are grossly understated and badly misleading. Consequently, although millions of wild birds constitute part of this wildlife trade annually, both legally and illegally, the trade in wild birds is thought to be as much as four times higher than what is recorded by the Convention on International Trade in Endangered Species of Wild Fauna and Flora, CITES (Beissinger 2001, Pain et al. 2006). Although parrots represent only a fraction of the trade in birds they are of significant commercial importance, as they constitute the most frequently traded species and are of comparatively high monetary value (Pain et al. 2006). This huge trade volume is driven by the high demand for parrots as pets and the accompanying economic gains for traders (Pires and Moreto 2011).

Rural communities in developing countries depend to a large extent on wildlife resources for both subsistence and income generation (Roe 2008, Sumukwo et al. 2013). Despite a wide variance in the estimated number of people dependent on wildlife resources for their income, as many as one billion people in the Asia-Pacific region alone are thought to have derived income, at least partially, from trade in non-timber forest products (Rijsoort and Pater 2000). The trade in wildlife thus potentially offers many benefits to the communities involved, particularly in terms of financial gain, and can significantly contribute to development if conducted legally and managed on a sustainable basis (Roe 2008). However, there is generally no equity amongst stakeholders with respect to the distribution of benefits accruing from the trade. For example, in Cameroon local trappers and 'middlemen' have been estimated each to receive less than 1% of what importers of the Grey Parrot obtain from the trade (Chupezi et al. 2006). Similarly, trappers in Ghana received an estimated 1–3% of the selling price of the Grey Parrot in the western world (Dändliker 1992).

1.2.3 The threat from habitat loss, degradation and fragmentation

The loss of and decline in the quality of habitats driven by, for example, logging and agricultural expansion are a major threat to the persistence of many bird species (93% or 1,146 species) (BirdLife International 2008c). The global situation is mirrored in Africa, where 75% and 49% of the 245 threatened bird taxa on the continent are directly impacted by agriculture and logging, respectively (BirdLife International 2013). Habitat fragmentation, which is intricately linked to habitat loss (Didham et al. 2012, Rueda et al. 2013), is capable of driving species extinctions even within protected areas (Andrén 1994). According to the World Resources Institute, nearly a third of global forest cover has been cleared and another 20% degraded, leaving the majority of remaining forest fragmented and only about 15% intact (http://www.wri.org/our-work/topics/forests).

The biology of the Grey Parrot is closely tied to forest habitats where the species finds resources for nourishment and reproduction (Juniper and Parr 1998, Dändliker 1992). The loss and degradation of tropical forests may result in the loss of important resources such as fruiting trees and potential nest cavities. Grey Parrots undertake local nomadic movements in search of food resources, and their survival stands to be compromised if essential feeding habitats vanish completely in relatively short periods. The availability of suitable nest-sites is a limiting factor for many parrot populations (Marsden and Jones 1997, Manning et al. 2013) because it can significantly reduce recruitment for subsequent years (Marsden and Pilgrim 2003, Pires 2012). This appears to have been a significant problem for the Grey Parrot in Ghana, where between the 1970s and 1980s 'salvage logging', which allowed the unlimited removal of supposedly 'over mature' and usually rotten trees from forest reserves (Hawthorne and Abu-Juam 1995, Benhin and Barbier 2004, Oduro et al. 2011), is likely to have impacted negatively on productivity in the species.

1.2.4 Other confounding threats to parrot populations

Other confounding factors contribute to the unfavourable conservation status of many species of parrot. Introduced species (often invasive) are a threat to native populations mainly because of competition with native species, for food and nesting resources (Juniper and Parr 1998, Wilson et al. 1998). Native species may not have natural defences against introduced species (e.g. mice, rats and cats) and their populations can be decimated through predation by the latter (Kuehler et al. 1997, Tatayah et al. 2007). The Mauritius Parakeet *Psittacula eques*, for example, was reduced to IUCN Critically Endangered status by predation from rats *Rattus rattus* and macaques *Macaca fascicularis*, and competition for nest-sites by the Common Myna *Acridotheres tristis* and Rose-ringed Parakeets *Psittacula krameri*, all of these species being non-native invasives (Tatayah et al. 2007, Jones et al. 2013, Jackson et al. 2015). Introduced species also have the potential to spread diseases to their native counterparts (Ortiz-Catedral et al. 2009, Kundu et al. 2012, Collar et al. 2015).

Parrots have a dietary predilection for seeds and fruits, and this results in crop raiding in certain areas, resulting in human-wildlife conflicts (Bucher 1992, Bomford and Sinclair 2002, Ribot et al. 2011). Monk Parakeet *Myiopsitta monachus* and Rose-ringed Parakeet are notorious agricultural pests and are often persecuted as a consequence. These species have been the subjects of many studies concerning their dietary and feeding habits (e.g. Ahmad et al. 2012, Canavelli et al. 2014). Besides suffering from the general threats to parrots, the Critically Endangered Yellow-crested Cockatoo *Cacatua sulphurea* has been persecuted as a crop pest in its native range in Indonesia (Trainor 2002).

Turbulent weather is a potential threat to parrot species with small ranges, especially insular species. For example, Imperial Parrot *Amazona imperialis* and Red-necked Parrot *A. arausiaca*, both endemic to the island of Dominica, have been frequently exposed to the vagaries of high-powered hurricanes over recent decades (Reillo and Durand 2008). Extreme weather conditions can seriously degrade habitat ;and result in the loss of suitable nest-sites (Christian et al. 1996). Shifts in climate patterns may also aggravate parrot population declines through the spread of other species such as nest-site competitors and predators (Sekercioglu et al. 2012).

1.3 A species in jeopardy: the notable case of the Grey Parrot in the pet trade

The *Psittacus* parrots of tropical Central and West Africa (Grey Parrot *P. erithacus* and Timneh Parrot *P. timneh*) are regarded as some of the most heavily traded bird species globally (Martin et al. 2014), and indeed are the most heavily traded of all parrots (Marsden and Royle 2015). Their great popularity can probably be attributed to their remarkable abilities to copy the human voice and indeed to interact meaningfully with their owners (Pepperberg 1994, 2006, Mulliken 1995, Collar 1997). These statistics put them in a special ‘niche’ of their own on the international market, with very high numbers sold both legally and illegally.

Grey Parrots—like most parrots—are long-lived and form long-term personal bonds with their keepers (Athan and Deter 2000, Schmid 2004). These close bonds are a matter of interest to many prospective pet owners, who are often oblivious to the challenges associated with the proper care and potential longevity of their pets. Many such individual pets end up in rescue homes (e.g. Engebretson 2006, Fronefield et al. 2008). Quite often, parrots can outlive their owners, or their owners simply lose interest in them owing to long-term maintenance problems (Schuppli and Fraser 2000). Grey Parrots do not have the usual very colourful and attractive plumage pigmentation found in many other parrot taxa, with the exception of the bright red tail (Collar 1997), but this is more than compensated for by their extraordinary abilities for mimicking human speech and other sounds, as well as their exceptional cognitive abilities (Pepperberg 1994, 2006).

A notable further circumstance of the *Psittacus* parrots, particularly *P. erithacus*, is their very large range (see below), formerly high densities, wide-ranging foraging movements and very poor levels of documentation and monitoring. These factors in combination mean that, although trade in these birds is seen as an economic right for the range states to exercise, localised population declines and extirpations are likely to have passed unnoticed, even if occurring on a wide scale. Trade regulators and conservation biologists face an exceptional challenge in determining what levels of offtake, if any, are now acceptable and sustainable in these species.

1.4 The biology of the Grey Parrot

1.4.1 Taxonomy and identification

Traditionally, the Grey Parrot has been regarded as a single species composed of two subspecies, *Psittacus erithacus erithacus* and *P. e. timneh*. However, the two taxa were recently split into two distinct species *P. erithacus* (Grey Parrot) and *P. timneh* (Timneh Parrot), respectively (del Hoyo and Collar 2014, BirdLife International 2015a, b). The separation of the hitherto monospecific genus, *Psittacus*, into two distinct species, is based on morphological differences and observed parapatry between the two taxa (del Hoyo and Collar 2014). Tobias et al. (2010) detail the system of quantitative criteria applied in the delimitation of the two parrot taxa as separate species. There is, however, now some evidence indicative of a blur across the line of parapatry of the two species in eastern Cote d'Ivoire owing to escaped birds from both sides of the zone (del Hoyo and Collar 2014). The insular subpopulation of Grey Parrot *P. e. princeps* on the island of Príncipe is treated as a separate race of *P. erithacus* (Melo and O'Ryan 2007, del Hoyo and Collar 2014).

The Grey Parrot differs from Timneh Parrot by having a paler grey plumage, a bright red tail as opposed to maroon, blackish rather than pinkish upper half of the upper mandible and a slightly bigger body size (15%) but with a less protracted central tail-tip (e.g. Dändliker 1992, Melo and O'Ryan 2007, del Hoyo and Collar 2014). Juvenile Grey Parrot chicks have dark (blackish) irides, which become paler with age. In immature birds, the iris colour becomes progressively paler grey before assuming a yellow hue that intensifies with further ageing. Adult Grey Parrots (about four years or older) have yellow irides of varying intensity, perhaps reflecting type and quality of nutrition (Dändliker 1992).

;21.4.2 *Distributional range, population trends and conservation status*

The distribution of the Grey Parrot extends across the lowland moist forests of West and Central Africa from south-eastern Côte d'Ivoire (near the Comoé River: Demey and Fishpool 1991) extending east, with a natural break at the rainforest-free 'Dahomey Gap' in Benin and Togo (Maley 1991, Dowsett-Lemaire and Dowsett 2014), through Cameroon and the Congo (Figure 1.1). The eastern boundaries extend to just east of the Albertine Rift (up to the shores of Lake Victoria) in Uganda and Kenya, and south to northern Angola (Juniper and Parr 1998). The species also inhabits the islands of Principe (Sao Tomé and Principe) and Bioko (Equatorial Guinea) (Melo and O'Ryan 2007). Substantial feral populations, often several hundred each, occur in Uganda (Martin et al. 2014), where breeding has been recorded in urban areas (Twanza and Pomeroy 2011, Irumba 2013).

The current global population of the Grey Parrot has been estimated to be between 0.56 and 12.7 million individuals (BirdLife International 2015a). However, this hitherto abundant and widespread species is believed on good evidence to have suffered major population declines in many parts of its range including Cote d'Ivoire, Ghana, Nigeria, Cameroon, parts of the Congo Basin and East Africa (Martin et al. 2014, BirdLife International 2015a, Marsden et al. 2015). Based on these declines, the IUCN has raised the conservation status of the species to 'Vulnerable' (BirdLife International 2015a, Marsden et al. 2015).

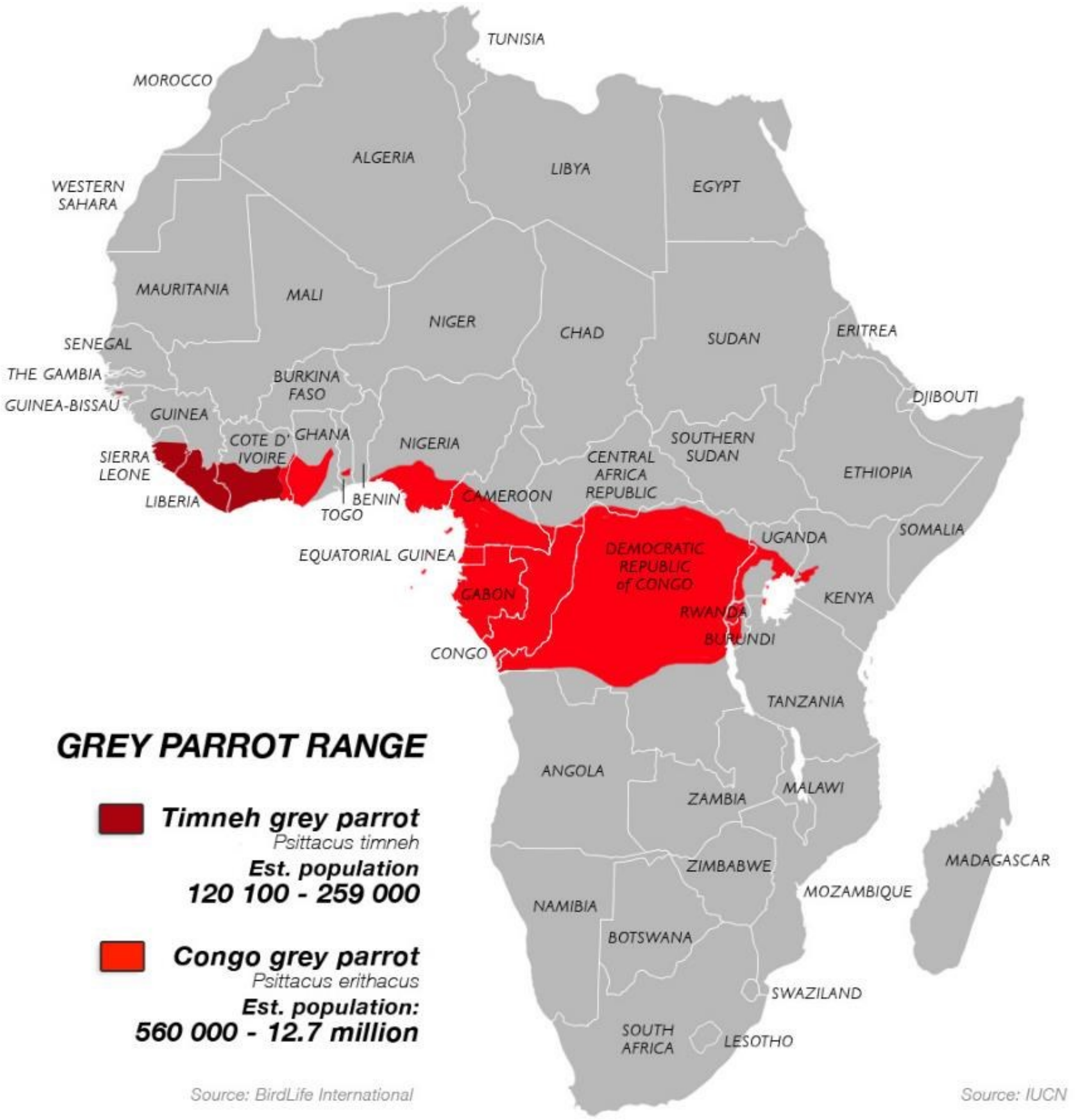

Figure 1.1: Map showing the ranges of Grey and Timneh Parrots sourced from the IUCN website. Note the difference in IUCN nomenclature for the two species.

1.4.3 Habitat requirements and general ecology

The Grey Parrot normally inhabits primary and tall secondary forest, but is commonly observed in a variety of other habitats including forest edge, clearings, gallery forest, mangroves, wooded savanna and cultivated areas (Collar 1997). However, these additional habitats appear generally to be used facultatively, providing some but not all of the conditions needed in the annual cycle. The species makes seasonal movements out of the driest parts of the range during the dry season, and occurs at altitudes of up to 2,200 m. The range is characterised by the prevalence of oil palm *Elaeis guineensis* (CITES 2006), the species' principal food source (Collar 1997).

The diet of the Grey Parrot is, however, very varied and includes fruits, seeds, flowers and buds from a broad array of tree species (Dändliker 1992, Chapman et al. 1993, Clemmons 2003, Dowsett-Lemaire and Dowsett 2014). The species also tends to prefer the hard parts of fruits as opposed to the fleshy parts, e.g. the seeds but not fruit of oranges. However, it prefers the flesh rather than the stone of the oil palm fruit. The fruits of other palms—raffia *Raphia* spp., coconut *Cocos nucifera* and borassus *Borassus* spp.—form a further important food source (Dändliker 1992). A reported case of geophagy in south-east Guinea (Clemmons 2003) conforms with other reports in Congo and Cameroon (Chapin 1939, Fotso 1996, May 2001). An isolated case of the ingestion of insect larvae was observed in Guinea, in addition to other reports regarding rice and beans on farmland in Guinea-Bissau (Clemmons 2003). On the other hand, old records of crop-raiding by the Grey Parrot in Ghana (Ussher 1874, Bannerman 1931) have been disputed recently (Dowsett-Lemaire and Dowsett 2014). *Psittacus* parrots characteristically access food items through acrobatic manoeuvres and dexterous manipulations using the feet and bill. They begin foraging from early morning until about 10h00 and again between 15h00 and dusk, when they return to roost. Trees in blossom with flowers and fruits can attract various numbers of parrots irrespective of their location such as near villages, field edges, protected forests and palm plantations (Dändliker 1992, Clemmons 2003, Tamungang and Ajayi 2003).

Psittacus parrots are social animals that spend a lot of time together in flocks, especially in periods when not breeding. The birds in an area assemble and roost overnight in flocks that number anything from a few pairs to several hundred individuals and, occasionally, a few thousand (Dändliker 1992, Clemmons 2003). However, with reports of massive population declines in most of the range states, such as in Ghana (Dowsett–Lemaire and Dowsett 2014, Martin et al. 2014, Marsden et al. 2015), it is most unlikely that roosts of such magnitude still occur in affected areas. Despite the gloomy outlook for these taxa, a flock of about 200 Timneh Parrots was recently observed in Sapo National Park in Liberia (Freeman 2014).

Breeding in Grey Parrots typically takes place during the dry season of the year (Forshaw and Cooper 1989, Dändliker 1992). The species normally nests in secondary tree cavities in forest habitats, but cliff cavity nests also occur (CITES 2013b). Breeding has also been observed in urban areas, including in buildings (Twanza and Pomeroy 2011, Irumba 2013). Breeding pairs form long-term bonds and females lay 1–4 (usually 2–3) eggs once per year with regional differences in laying dates (Benson et al. 1988). Incubation and fledging both take about 30 days (Juniper and Parr 2003) and the fledglings leave the nest after about 80 days (Collar 1997).

1.5 The Grey Parrot in Ghana

The Grey Parrot occurred over nearly the whole of Ghana's high forest zone (HFZ), as well as parts of the transition zone habitats between the rainforest (southern Ghana) and the savanna (northern Ghana) (Grimes 1987, Dändliker 1992). The species was also present in riparian forests in the savanna regions of the country (Dändliker 1992). It generally prefers riverine swamps with *Raphia* palms and bamboo (various genera) in the HFZ within the Ghanaian range, but it also commonly forages and roosts in *Elaeis guineensis* plantations (Dändliker 1992). Grey Parrots were common and roosts of several hundred birds were reported mainly in the south-west of the country. However, further north or east of the HFZ the species was less common and was considered absent from the easternmost parts of southern Ghana—a region with potentially suitable Grey Parrot habitat (Dändliker 1992). The absence of the Grey Parrot from these easternmost forests of Ghana may be attributable to the latter's small size and isolation from the wet HFZ, where the majority of parrot populations are located (Dändliker 1992). However, there are small populations of Grey Parrot in the relatively well-wooded but small areas within the national capital, Accra (Grimes 1987, Dändliker 1992). These populations are thought to be feral (Dändliker 1992, Dowsett-Lemaire and Dowsett 2014), but they were evidently present at least as early as 1960 (Bouet 1961).

In Ghana, the Grey Parrot breeds during the dry season (typically November–February) and the progeny fledge prior to the rains (Dändliker 1992), as in other parts of the range (Forshaw and Cooper 1989). The species nests in tree cavities 10 m or more above ground. Nest size was found to be 0.033–0.119 m^3 based on three sampled cavities (Dändliker 1992). Grey Parrot nest cavities are commonly found in large tall trees (including snags) of *Ceiba pentandra*, *Terminalia superba*, *Triplochiton scleroxylon*, *Celtis mildbraedii*, *Chlorophora excelsa*, *Antiaris africana*, *E;2ntandrophragma angolense* and *Distemonanthus benthamianus* (Dändliker 1992).

Despite the sense in the 1940s that the species might have been declining in some areas owing to trade, aggregations of 500–1,000 parrots could then still be observed (Grimes 1987). About forty years on (1988), large flocks of 2,000–3,000 could still be observed in parts of the parrot's range in Ghana (Dändliker 1992). Data from studies between 1976 and 1978 conducted by the Ghana Wildlife Division (GWD) in and around the village of Achiase (Aykease) in the Central Region, and analysed by Dändliker (1992), produced an average Grey Parrot encounter rate of 7.4 birds per morning. Fifteen years after the GWD studies, Dändliker (1992) recorded Grey Parrot encounter rates of 5.3 birds per morning near the Achiase area.

By 1992, around 60 Grey Parrot roosts (although perhaps not all active at one time) had been identified within Ghana, distributed throughout the forest zone, with the distance of any given roost to the three nearest roosts averaging 27 km; altogether 130–210 roosts were thought to exist within the forest zone (Dändliker 1992). Roost density was estimated at 0.18–0.27 per 100 km^2 and, allowing for varying abundances in different forest types, the national population was extrapolated as 30,000–80,000 Grey Parrots (Dändliker 1992). In a multi-species forest bird study between June 1995 and August 1996, Grey Parrots were found in "more than 20" of the 28 forest reserves studied, but only 87 groups were recorded during the entire survey period (Ntiamoa-Baidu et al. 2000).

Large numbers of Grey Parrots were already for sale in Accra and Cape Coast in the 1870s (Dowsett-Lemaire and Dowsett 2014), and trade with Ghana's neighbours in Grey Parrot body parts is thought to have begun in the mid-1970s (Dändliker 1992). In the early 1970s, Hajj pilgrims from Ghana to Mecca began the export of Grey Parrots to Saudi Arabia, for resale (Dändliker 1992). This newly discovered but lucrative trade was not monitored by the Ghanaian authorities and involved the export of large numbers of parrots: at the peak of the trade up to 20,000 birds annually crossed Ghana's borders without documentation by air, in both the cabin and cargo hold. This novel trade route thrived until Saudi Arabia banned the importation of parrots in 1986 (Dändliker 1992). Meanwhile, several thousand Grey Parrots were illegally exported annually across Ghana's borders to countries such as Côte d'Ivoire, Togo, Mali and Benin, as far as Senegal, for re-export to Europe and the USA (Dändliker 1992). However, the Grey Parrot trade was banned several times in Ghana after 1967, including in May 1980 when the government placed an embargo on exports owing to suspicions that the species was being used to smuggle diamonds (Dändliker 1992). These bans were repeatedly imposed and revoked between 1980 and 1989, until the last ban was triggered by CITES regulations in 1994. This last ban is still in force, owing to lack of data for establishing an export quota (CITES 2012).

According to Dowsett-Lemaire and Dowsett (2014), the current distribution of the Grey Parrot has contracted and become patchier in Ghana over the past several decades, and the species is currently seriously threatened in the country by habitat loss and capture for the pet trade.

1.6 Grey Parrot conservation: challenges and opportunities

1.6.1 The significance of parrots and other large avian frugivores to ecosystem function

The various threats to the survival of large avian frugivores such as habitat loss, hunting and trapping for food and the international pet trade have led to significant population declines in many tropical species, and even some extinctions (Butchart et al. 2010, Fernandes-Ferreira et al. 2012 Española et al. 2013). These marked declines in the abundance of species, and the extinction of others, can result in significant negative ecological impacts on communities through such factors as the spread of disease, loss of agricultural pest control, plant extinctions and trophic cascades. Such devastating events may trigger considerable deterioration in certain ecosystem processes before scientists have the opportunity to study and understand the underlying mechanisms or appreciate their importance (Sekercioglu et al. 2004). For example, the loss of keystone frugivore species such as hornbills, which play vital roles in forest tree composition and distribution (Redford 1992, Kinnaird and O'Brien 2007, Trail 2007), ultimately alters the structure and function of the forests they inhabit and potentially causes irreversible ecological imbalances, with negative repercussions for forest regeneration (Higman et al. 1999, Sodhi et al. 2008, Kitamura 2011).

Species that destroy the seeds of fleshy fruits (seed predators) cause both pre- and post-dispersal loss of seeds (Villaseñor-Sanchez et al. 2010). Pre-dispersal seed predation occurs when fruits and/or their seeds are removed from the parent plant prior to dispersal, whereas post-dispersal seed predation occurs subsequent to the spread of propagules from the parent plant. Parrots, certain pigeons and finches fall within the former category of consumers (Janzen 1981, Lambert 1989, Corlett 1998). Seed predation can be detrimental but also advantageous in some cases when seed predators act as biological control agents against the spread of exotic plant species (Nunez et al. 2008). Parrots could potentially cause relatively high rates of pre-dispersal seed predation. For example, in a Mexican study of Lilac-crowned Parrots *Amazona finschi*, Villaseñor-Sanchez et al. (2010) found that the parrots could prey on up to 56% of seeds prior to dispersal.

Even so, contrary to the long-held view that parrots are generally seed-predators and do not engage in seed dispersal mutualisms (e.g. Galetti and Rodrigues 1992), a recent study showed that as many as 28 species of parrot actively contribute to seed dispersal in many plants (98 plant species in seven countries studied, Tella et al. 2015). In the valleys of the Bolivian Andes, Blanco et al. (2015) also found that parrots engaged in various trophic interactions that involved many mutualistic relationships with 113 species from 38 plant families. A more thorough evaluation of parrot-plant interactions in general could yield valuable information that may change the contemporary view of psittacines as being predominantly plant antagonists (Blanco et al. 2015, Tella et al. 2015).

1.6.2 Challenges to accurate population assessments for conservation purposes

Population size estimation and regular population monitoring are vital prerequisites to the meaningful formulation and implementation of any parrot conservation efforts (Snyder et al. 2002, Martin et al. 2014b). Such monitoring is also necessary for determining trade quotas in line with international trade regulations (CITES 2007), which in turn take sustainability of harvests into consideration. However, efforts to survey populations of the species are fraught with challenges, including methodological difficulties (e.g. McGowan 2001) and the colossal task of estimating accurate population densities across the entirety of the species' range.

First, the large range of the Grey Parrot makes it impracticable to conduct complete population surveys simultaneously, as such efforts require extensive and expensive logistical provisions. Moreover, severe declines have occurred in many parts of the range (CITES 2013b, Martin et al. 2014a), and the current patchiness in distribution (Marsden et al. 2015), as well as the concomitant variability in densities, means that extrapolation of local population estimates will not yield accurate population sizes over appreciably wider areas (Martin et al. 2014b). Furthermore, Grey Parrot characteristics such as the tendency to be quiet and cryptic when feeding, the formation of large social aggregations that make them unevenly distributed, and the common habit of performing long-distance flights between feeding and roosting sites, pose challenges that constrain accurate population estimates for the species (Marsden et al. 2015).

1.6.3 International and local regulations

Declining populations of heavily traded wildlife species have necessitated the institution of both international and national regulatory schemes, with the broad aim of ensuring the sustainable use and long-term conservation of the species involved. Managing the threats posed by the movement of wildlife species and their derived products across borders forms part of this broad aim (Roe et al. 2002, Roe 2008, Pires and Moreto 2011). Several international regulatory schemes have been acceded to by interested parties since the early 1900s, but the CITES convention (CITES 2013a) has been the main multilateral agreement pertinent to the regulation of the international trade in wildlife (Roe et al. 2002, Roe 2008, Wyler and Sheikh 2008). CITES defines the legal framework for the trade and relies on member states to formulate and implement national legislation in conformity with this framework. All species of plants and animals under CITES control are placed within three categories referred to as Appendices I, II and III. Trade in species belonging to each of these categories is controlled by sets of rules. Appendix I invokes the most stringent trade control measures, and essentially bans trade in the species it lists (see Articles III-V of the text of the convention, https://cites.org/eng/disc/text.php). Appendix II allows for trade on condition that parties establish quotas and report imports and exports honestly and accurately. Appendix III is for individual countries to list species as they see fit for the purpose of preventing or restricting exploitation. Parties thereby commit to ensuring the sustainability of populations within their respective jurisdictions. Nonetheless, national-level statutes for the regulation of the trade in many countries pre-date the CITES agreement. Furthermore, there are traditions and customary practices in many countries aimed at the management of natural resources including wildlife. Even though the regulation of the trade in wildlife and their products has had some successes, it has not always yielded the desired results (Hutton and Dickson 2000).

The difficulty in quantifying and controlling the trade in wildlife is mainly due to its clandestine nature, as much of it is conducted illegally or through informal networks that are difficult to track (Karesh et al. 2005) and hence difficult to control, sometimes involving corrupt officials of regulatory bodies. The trade in wild (bush) meat, for example, although an important source of income and a major contributor to food security, remains primarily illegal, clandestine and unmanaged (Roe 2008). Strict methods of tackling the illegalities surrounding the trade by means of law enforcement, such as through police crackdowns, typically do not yield long-term results. This is mainly because such crackdowns are temporary and offenders resume their activities as soon as law enforcement agents reduce or withdraw their efforts (Pires and Moreto 2011). The scope, sophistication and organisation of the wildlife trade are considered to have been growing in recent times, and in some cases traffickers are known to be linked to international syndicates (Wyler and Sheikh 2008).

1.6.4 The need for sustainability assessments

Generally, the extraction of wildlife resources can only be sustained if offtake is within the limits of productivity levels (Slade et al. 1998, Robinson and Bennett 2004). To ensure this is the case, source populations must undergo periodic sustainability assessments to inform decision-making on offtake limits. Such assessments should, of course, be underpinned by scientifically derived data on population trends, population viability or both. Under Article IV of CITES these assessments provide the evidence for non-detriment findings (NDFs) to be made for Appendix II-listed species before harvest quotas can be granted. Any NDF should provide adequate information for decision-making on the potential effects of trade by examining various aspects of the conservation status of the species in question, such as their distribution, biology, population trends and trade levels (Natusch and Lyons 2012). Population viability analysis (PVA), which is a process that involves the evaluation and modelling of pertinent data in order to predict the probability of persistence of a population over time

(Boyce 1992, 1993), can be useful in this respect. PVA has come under criticism by some researchers (Ellner et al. 2002), but others have fiercely defended it and highlighted its versatility (Brook et al. 2002).

However, there is a multiplicity of models to support the theory of harvesting wildlife resources from the wild, the basis for which is the concept of Maximum Sustained Yield (MSY). The MSY can be defined as the largest harvest that can be taken from a population indefinitely without driving the population to extinction (van der Heijden 2003). Regrettably, the biological data required to run the various population analyses for sustainable harvests are, in reality, unavailable, and the determination of sustainability is thus reduced to a process of trial and error (van der Heijden 2003). Furthermore, the lack of real harvest data due to illicit trading makes sustainability assessments difficult. To circumvent the problems associated with quantitative assessments for establishing NDFs, the IUCN applies a qualitative approach that focuses on factors which could affect the sustainability of extraction and therefore need consideration in establishing extraction levels (van der Heijden 2003).

Commercial trade in the Grey Parrot has undergone several periods of embargo in Ghana since 1967, often for reasons of conservation concern, albeit needless to state that these embargoes have been lifted nearly as many times (Dändliker 1992). Today, however, the trade ban remains in force in Ghana owing to the lack of adequate data for establishing an export quota, with all exports ceased since the mid-1990s (CITES 2012). Cameroon, by contrast, successfully obtained an export quota for 3,000 Grey Parrots from CITES in 2012 (IISD 2012), based on a population status study and a species management plan (Tamungang and Cheke 2012).

Despite the trade ban on the export of Grey Parrots in Ghana and the existence of legal provisions for the protection of wildlife in general (e.g. Wild Animals Preservation Act of 1961 and its subsequent amendments), the distributions and populations of several species of frugivores appear to have declined, probably owing to hunting, habitat change and/or modification (Dowsett-Lemaire and Dowsett 2014). Ghana lost an enormous amount (90%) of its forest cover in just half of the last century alone (http://rainforests.mongabay.com/20ghana.htm). The country's deforestation rate has been estimated at 650 km^2 per annum (World Bank 2007) and continues to escalate (Marfo 2010). Poor forest management strategy, fire, mining and quarrying act in concert with logging and farming as the major causes of deforestation and forest habitat alteration in the country (Benhin and Barbier 2004).

The existing state of affairs necessitates the determination of the current distribution of species and species richness in what is left of Ghana's forest estate, and the identification of the main factors that drive these distributions and changes. The information derived will, in turn, enable the identification of important areas for concerted conservation action, and point towards those factors that need prioritised management from a conservation perspective. The use of species distribution modelling lends itself to this task (see e.g. Elith and Leathwick 2009).

1.7 Species distribution modelling: a major tool for conservation planning

Species distribution models (SDMs) are quantitative methods which associate the occurrence of a species at multiple locations with environmental variables to predict distributions based on estimates of the suitability of sites where the species is likely to occur (Carpenter et al. 1993, Fielding and Bell 1997, Wisz et al. 2008, Elith and Leathwick 2009). SDMs are a fast-growing field of research (Brotons 2014), and have variously been referred to as ecological niche modelling, climate envelope modelling and habitat suitability modelling (Elith and Graham 2009, Duan et al. 2014). SDM techniques have been applied extensively in various disciplines such as ecology, biogeography, biodiversity conservation and natural resource management (Guisan and Thuiller 2005, Newbold 2010, Franklin 2013, Guisan et al. 2013) specifically for the management of threatened species, effects of climate change on species distributions, studies on phylogeographic patterns and the management of landscapes (Guillera-Arroita et al. 2015).

There has recently been a marked sophistication and proliferation of SDM techniques (Phillips et al. 2004, Segurado and Araújo 2004, Elith et al. 2006, Guillera-Arroita et al. 2015), a few examples of which are Environmental Niche Factor Analysis (ENFA), Multivariate Adaptive Regression Splines (MARS), Genetic Algorithm for Ruleset Prediction (GARP), and Maximum Entropy (Maxent). The sophistication and proliferation of SDMs is attributable to the application of machine-learning principles in the development of many of these SDMs. Machine-learning refers to the methods by which computers 'learn' without being explicitly programmed (Samuel 1959). These methods apply algorithms which automatically recognise complex patterns in datasets, and enable the computer to arrive at intelligent conclusions.

One machine-learning principle that has seen extensive application in the development of SDMs is that of Maximum Entropy (Phillips et al. 2006). This principle states that, subject to precisely stated prior data, the probability distribution that best represents the current state of knowledge is the one with largest entropy (Jaynes 1957a, b). Entropy, in this context, refers to a probability-based measure of 'dispersedness' (Elith et al. 2011). One product of the application of the maximum entropy principle in SDMs is the MaxEnt programme (see Phillips et al. 2004, Phillips et al. 2006, Elith et al. 2006). Among various SDM techniques currently available, MaxEnt is widely used owing to its accuracy and simplicity in predicting species distributions (Elith et al. 2006, Heikkinen et al. 2006, Hernandez et al. 2006, Wisz et al. 2008, Warren and Seifert 2011). An inherent assumption of the programme is that species without ecological barriers disperse uniformly (Duan et al. 2014). MaxEnt is a presence-only SDM technique that does not forecast abundance measures such as species densities or encounter rates, but has seen enormous use in the prediction of species ranges and changes in range (e.g. Marin-Togo et al. 2012) and habitat suitability assessments for species reintroductions (Thorn et al. 2009). While not intrinsically useful for abundance measurements, MaxEnt can contribute to IUCN Red List assessments by providing information on specifics such as extent-of-occurrence and area-of-occupancy metrics (Marsden and Royle 2015).

1.8 Overall aim of the PhD and objectives of chapters

Academic aim

The aim of the PhD is to assess the historic and current distribution, abundance and ecology of western populations of the Grey Parrot, where possible using novel study methods, in order to make informed predictions about the sustainability of trade and land-use changes. Relevant information on other frugivores impacted in ways similar to Grey Parrot are also considered.

List of objectives

1. To describe and explain differences in avian frugivore community composition and abundance across Ghana.

2. To identify likely areas of occupancy for the large frugivorous birds of Ghana, the strongest environmental predictors of their current distributions, and, ultimately the most important areas for focused conservation action.
3. To use roost location surveys and counts of birds at roosts/roost areas across Ghana to determine population sizes and densities, and changes in populations over time.
4. To use Maxent Species Distribution Modellig to track decadal changes (*circa* 1990–2012) in the distribution of the Grey Parrot across Ghana.
5. To use the results from 1–4 above in making informed predictions about the likely sustainability of parrot populations across the western range in relation to trade and habitat change.

Scope of analysis chapters

- *Chapter 2: Frugivore communities and abundance across Ghana*

In Ghana, many large avian frugivores face various threats to their survival including habitat loss, hunting and trapping for food and the international pet trade. However, information is lacking on the distribution and abundance of most avian frugivores. To investigate patterns of occurrence and abundance across the country, I conducted transect surveys for twenty frugivore species of pigeons, parrots, turacos and hornbills in 42 squares each of 10 km × 10 km area in and around forest reserves in south-west Ghana. I assessed frugivore diversity in the study area and performed Canonical Correspondence Analysis (CCA) to identify the main drivers or environmental gradients influencing bird community make-up.

- *Chapter 3: Distribution modelling for large avian frugivores across Ghana*

Large avian frugivores are important both for biodiversity conservation and as ecosystem service providers. However, many species have declined across much of West Africa. To identify the probable areas of occupancy (AOO) for the large frugivorous birds of Ghana, the likely environmental drivers of their current distributions, and important areas for focused conservation action I used Maxent—a presence-only species distribution modelling technique—to predict the distribution and probability of occurrence of 15 species of parrot, hornbill, pigeon and turaco across Ghana.

- *Chapter 4: Collapse of Grey Parrot populations in Ghana*

The heavily traded Grey Parrot *Psittacus erithacus* is believed to have undergone rapid population decline, yet there are almost no quantitative data on abundance changes over time from anywhere within its huge range. To address this knowledge gap, I reviewed the species' historical abundance across Ghana, undertook targeted searches during 3–5 day visits to forty-two 100-km^2 cells across the country's forest zone, repeated counts at 22 parrot roosts first performed two decades ago and gauged around 900 people's perceptions of the decline and its causes.

- *Chapter 5: Spatiotemporal changes in Grey Parrot distribution and abundance in Ghana*

Over the past two decades or more, Grey Parrots may have declined by up to 99% in Ghana, but paradoxically remain reasonably widely distributed in the country. I developed species distribution models (SDMs) with Maxent for the species based on records from the early 1990s ('historical') and 2010 onwards ('current'). Presence records came from 1. Actual field surveys performed by Dändliker (1992) and my own fieldwork in 2012–14; 2. The Global Biodiversity Information Facility (GBIF) based on visiting birdwatchers' records (current); and 3. Interview data where respondents were asked when they last observed Grey Parrots. Environmental layers were land use, rainfall and rainfall seasonality, EVI, net primary productivity and human population density.

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Chapter 2

FRUGIVORE COMMUNITIES AND ABUNDANCE ACROSS GHANA

2.1 Abstract

Marked declines in the abundance of bird species, including avian frugivores, and their inevitable extinction can result in significant negative ecological impacts on communities such as the spread of disease, loss of agricultural pest control, plant extinctions and trophic cascades. Such devastating events may trigger considerable diminutions in certain ecosystem processes before scientists have the opportunity to study and understand the underlying mechanisms or appreciate their importance. In Ghana, many large avian frugivores face various threats to their survival including habitat loss, hunting and trapping for food and the international pet trade. However, there is no empirical knowledge on the distribution and abundance of most avian frugivores. To investigate patterns of occurrence and abundance across the country, I conducted transect surveys for twenty frugivore species of pigeons, parrots, turacos and hornbills in 42 squares each of 10 km × 10 km area in and around forest reserves in southwest Ghana. I assessed frugivore diversity in the study area and performed Canonical Correspondence Analysis (CCA) to identify the main drivers or environmental gradients influencing bird community make-up. Frugivore species richness varied across study sites from two to 15 species. The most abundant species, West African Pied Hornbill *Lophoceros semifasciatus* and African Green Pigeon *Treron calvus*, were recorded in nearly all study sites. The most restricted and rare species included large-bodied species such as Great Blue Turaco *Corythaeola cristata*, Yellow-casqued Hornbill *Ceratogymna elata* and Black-casqued Hornbill *C. atrata*. The CCA showed that large-bodied hornbills and a few other species tended to occur in large

reserved forest with low anthropogenic disturbance. Many large avian frugivores in Ghana are not common or widely distributed. The large hornbills *Ceratogymna spp*., *Bycanistes subcylindricus*, turaco *Corythaeola cristata*, and parrot *Psittacus erithacus*, may have suffered range contractions owing to habitat loss and hunting. Enhanced protection by way of increased guard patrols in forest reserves with remnant frugivore populations coupled with active conservation education in satellite communities, and changes in logging practices are, urgently needed to prevent the inevitable extinction of frugivores in Ghana.

2.2 Introduction

2.2.1 Ecosystem importance of frugivores

Birds are notably one of the best-known assemblages of organisms (Sekercioglu 2006) as their ecology, taxonomy and global geographical distributions are comparatively well documented with respect to other taxa (Schulze et al. 2004, Gray et al. 2007, BirdLife International 2012b). In view of the general ecological importance of birds (Sekercioglu 2006) frugivores, especially, perform vital ecosystem functions that include the maintenance of forest structure (Cordeiro and Howe 2001, Sodhi et al. 2008, Kankam and Oduro 2009, 2012). For example, many forest-inhabiting hornbills are important seed dispersers (Whitney and Smith 1998, Whitney et al. 1998, Holbrook and Smith 2000, Kinnaird and O'Brien 2007). Furthermore, frugivores are also functionally important in several ways, as when they mediate the escape of seeds from seed predators through dispersal, improve seed germination through digestive processes, increase economic yield from farm produce and increase gene flow through seed dispersal and pollination (Sekercioglu et al. 2004, Sekercioglu 2006).

2.2.2 *Frugivore diversity and make-up in the tropics*

In a global-scale analysis to assess the incidence of bird frugivory in relation to cladistics, biogeography and environmental factors Kissling et al. (2009) identified 1,230 avian frugivores out of a total 8,918 terrestrial bird species (13.8% or just over one-sixth). Of these 1,230 frugivores there are 179 pigeons, 141 parrots and cockatoos, 48 cracids, 48 toucans, 38 hornbills, 23 turacos and 15 trogons in addition to several other groups. There are also some 71 predominantly frugivorous species of cotinga and numerous species of barbet (Snow 1981, Short and Horne 2002). Avian frugivore species richness is far higher in the tropics than in temperate regions, and richness is also even within the tropics, where the Neotropics is richer than the Indo-Malaya region, which is in turn richer than the Afrotropics (Kissling et al. 2009). There is a particular preponderance of avian frugivores in the Wallacean and Papuan regions, areas which generally lack primates (White and Bruce 1986). The majority of avian frugivores are found in habitats with high plant species richness that are characterised by an abundance of fleshy fruits (Snow 1981, Gentry 1982). The high species richness of fleshy-fruited plants in the Neotropics therefore explains the proportionately high species richness in frugivorous birds.

Many large avian frugivores face various threats to their survival including habitat loss, hunting and trapping for food and the international pet trade. This has led to significant population declines and extinctions in many tropical species (Española et al. 2013). Marked declines in the abundance of bird species, including avian frugivores, and the inevitable extinction of others can result in significant negative ecological impacts on communities such as the spread of disease, loss of agricultural pest control, plant extinctions and trophic cascades. Such devastating events may trigger considerable diminutions in certain ecosystem processes before scientists have the opportunity to study and understand the underlying mechanisms or appreciate their importance (Sekercioglu et al. 2004). For example, the loss of keystone frugivore species such as hornbills which play vital roles in forest tree composition and distribution (Redford 1992, Kinnaird and O'Brien 2007, Trail 2007) ultimately alters the structure and function of the forests they inhabit and potentially causes irreversible ecological imbalances with negative repercussions for forest regeneration (Higman et al. 1999, Sodhi et al. 2008, Kitamura 2011).

Various studies have assessed the drivers or gradients that influence avian community composition and structure (Beier et al. 2002, Kissling et al. 2007, Newbold et al. 2013, Española et al. 2013). In their study of the effects of forest habitat characteristics on forest birds, Beier et al. (2002) suggested that in West Africa species richness could decline as much as 25% because of forest fragmentation. In a study that considered avian species presence and abundance data from all over the tropics, Newbold et al. (2013) found that species richness and the abundance of large-bodied, long-lived, non-migratory, mainly forest specialist frugivores generally declined with increasing anthropogenic habitat disturbance. In the Philippines, Española et al. (2013) indicated that the high level of avian diversity and endemism is attributable to a wide range of habitat types that derive from the long history of the archipelago, as well as environmental factors (Española 2013). They also, however, suggest that anthropogenic habitat alterations have masked biogeographical boundaries, with potential loss of large frugivores. Kissling et al. (2007) however, explain that in sub-Saharan Africa the diversity of food plants is a major determinant of avian species richness.

Ghana is rich in avian frugivores, having high diversity in parrots (7 species), turacos (5), hornbills (12, with small to medium-sized species mainly omnivorous) as well as two exclusively frugivorous species among 17 pigeons (Baptista et al. 1997).

The Upper Guinea forest ecosystem of which Ghana forms a part is rich in endemics (15 restricted-range species 11 of which are threatened). Two species of hornbill (Brown-cheeked Hornbill *Bycanistes cylindricus* and Yellow-casqued Hornbill *Ceratogymna elata*) as well as the Grey Parrot *Psittacus erithacus* are in the IUCN Red List category of 'Vulnerable' species. The main threats to these species are apparently forest fragmentation and loss, and hunting for food and/or the pet trade (BirdLife International 2008a, 2008b, 2012a, 2013, Dowsett-Lemaire and Dowsett 2014). However, there are very few up-to-date quantitative data on population sizes and trends, extent of offtake from the wild, and/or habitat associations to support these assessments (Marsden and Royle 2015).

Avian frugivore ecology has not been a major part of the focus of biological research in Ghana. Lieberman and Lieberman (1986) found no significant effects in an experimental study examining the effects of fruit ingestion on seed germination by three large and three small frugivores. Kankam and Oduro (2009, 2012) found one bulbul plus a number of larger frugivores (including a barbet, turacos and hornbills) to be important to seed dispersal and germination in one timber tree species. Deikumah et al. (2013, 2014) demonstrated that mining activities have a negative impact on avian frugivores. Dowsett-Lemaire and Dowsett (2014) mapped frugivore species distributions on a 30×30 km^2 grid and found marked contractions in the distribution of many avian frugivores, with concomitant declines in species abundance, especially in many hornbill and parrot species.

The lowland forests stretching from Guinea and Sierra Leone eastward to the Sanaga River in Cameroon comprise what are referred to as the Guinean Forest biome of West Africa (CEPF 2000, Figure 1). They encompass Liberia, Côte d'Ivoire, Ghana, Togo, Benin and Nigeria, albeit only as relics (15%) of the original extent of the biome.

This biome has a high degree of diversity and endemism in birds generally (CEPF 2000), including large frugivores such as the Brown-cheeked Hornbill (BirdLife International 2014). It is interrupted in Benin by a mosaic of savanna, farmland and heavily degraded dry forest called the Dahomey Gap (Collett and Primack 2011), and the faunas and floras west ('Upper Guinea') and east ('Lower Guinea') of this gap, although sharing many similarities, have some important differences (Conservation International 2013).

With a land area of 238,589 km^2, Ghana has one of the highest human population growth rates in the world and has a population doubling time of about 26–29 years compared to 170 years for developed countries. This phenomenon is mainly due to high fertility rates dating back over a long period (National Population Council of Ghana 2006, 2011). Ghana's latest census in 2010 recorded a population size of 24.6 million people, indicating that the country's population density has increased from 52 people per km^2 in 1984 to 103 in 2010 (Ghana Statistical Service 2012). In Ghana, a multiplicity of anthropogenic activities affects the integrity of both reserved and unreserved forests. The operations of companies engaged in large-scale surface mining have directly resulted in the loss of vast areas of forest cover (Manu et al. 2004, Akpalu and Parks 2007, World Bank 2007, Luginaah and Yanful 2009, Schueler et al. 2011). The proliferation of artisanal small-scale mining over the past few decades is also a major contributor to forest loss and degradation, with operations rife in and around many forest reserves (Donkor and Vlosky 2003, Schueler et al. 2011). Deforestation and forest degradation through unsustainable logging, legal and illegal (Eshun et al. 2010), as well as poor farming practices such as slash-and-burn shifting agriculture, have taken a heavy toll on Ghana's forests (Holbech 2009, Appiah et al. 2010). Hunting also contributes significantly to forest degradation and loss in Ghana owing to forest fires. It is commonplace for hunters to fell a tree in order to trap arboreal species such as tree pangolin and tree hyrax (author pers. obs.). In extreme cases, hunters set fire to trees in order to capture their bounty, thus inadvertently causing forest wildfires (Ampadu-Agyei 1988, Nsiah-Gyabaah 1996, Ntiamoa-Baidu 1997).

The forest zone of Ghana covers just over a third of the country's land area, approximately 81,000 km^2 (Nketiah et al. 2004, Aryeetey et al. 2006, Adam et al. 2006). These relic forests, which comprise of a network of reserved areas, represent approximately 25% of Ghana's original forest cover (Nketiah et al. 2004); they form part of the Upper Guinea Forests, the block of forest biome west of the Dahomey Gap (Kouame et al. 2012). In Ghana, the land area degraded by agricultural activities keeps expanding owing to the extensive farming systems practised. Slash-and-burn cultivation, for example, aggravates the problem and results in forest depletion and loss of biodiversity in affected areas (Aryeetey et al. 2006). Generally, protected areas are expected to serve the dual function of promoting ecological stability and guaranteeing the supply of goods and services (Bird et al. 2006), but although Ghana currently possesses over 200 legally protected forests deforestation continues unabated in both protected and non-protected areas (Alo and Pontius 2008, Holbech 2009).

2.2.3 Aim and objectives

The aim of this chapter is to describe and explain differences in avian frugivore community composition and abundance across Ghana. To achieve this aim I have the following objectives:

1. To investigate patterns of occurrence and abundance of individual frugivore species across the country.

2. To identify the main drivers or gradients influencing the frugivore community make-up.

2.3 Methods

2.3.1 Study area and bird surveys

Frugivore abundance surveys were conducted in the high forest zone (HFZ) of Ghana for 20 avian frugivores (Table 2.1) through roost and transect counts throughout the southwest of the country between April 2012 and June 2014 (Figure 2.1). The HFZ was subdivided into a grid of 10 km × 10 km cells and a sample of 42 cells was selected for surveys. The survey sites were selected in a manner that maximised the probability of encountering frugivore populations. This approach to site selection was not random, but was based on the presence of substantial forest cover. The variety of habitat types surveyed were forest reserves in protected areas, mosaics of old fallow and degraded forest remnants, small-scale agricultural ecosystems, and neighbouring habitats of countryside settlements. Other surveyed habitats were large-scale oil palm *Elaeis guineensis* and cocoa *Theobroma cacao* plantations, as well as swampy areas characterised by bamboo *Bambusa spp*. and raffia palms *Raphia spp*. Each cell was visited for periods of 3–5 days and surveys were conducted daily between 05h45 and 11h00. Surveys were carried out by walking along hunter or farmer footpaths and along drivable pathways connecting villages or towns. Survey routes were walked in the company of a local guide, and all individual birds encountered along the route were recorded as perched or in flight, and where applicable, the direction of flight. Additionally, long watches were conducted from vantage positions between 16h00 and 18h00 on some days, timed to correspond with the period of late afternoon flight towards roosts.

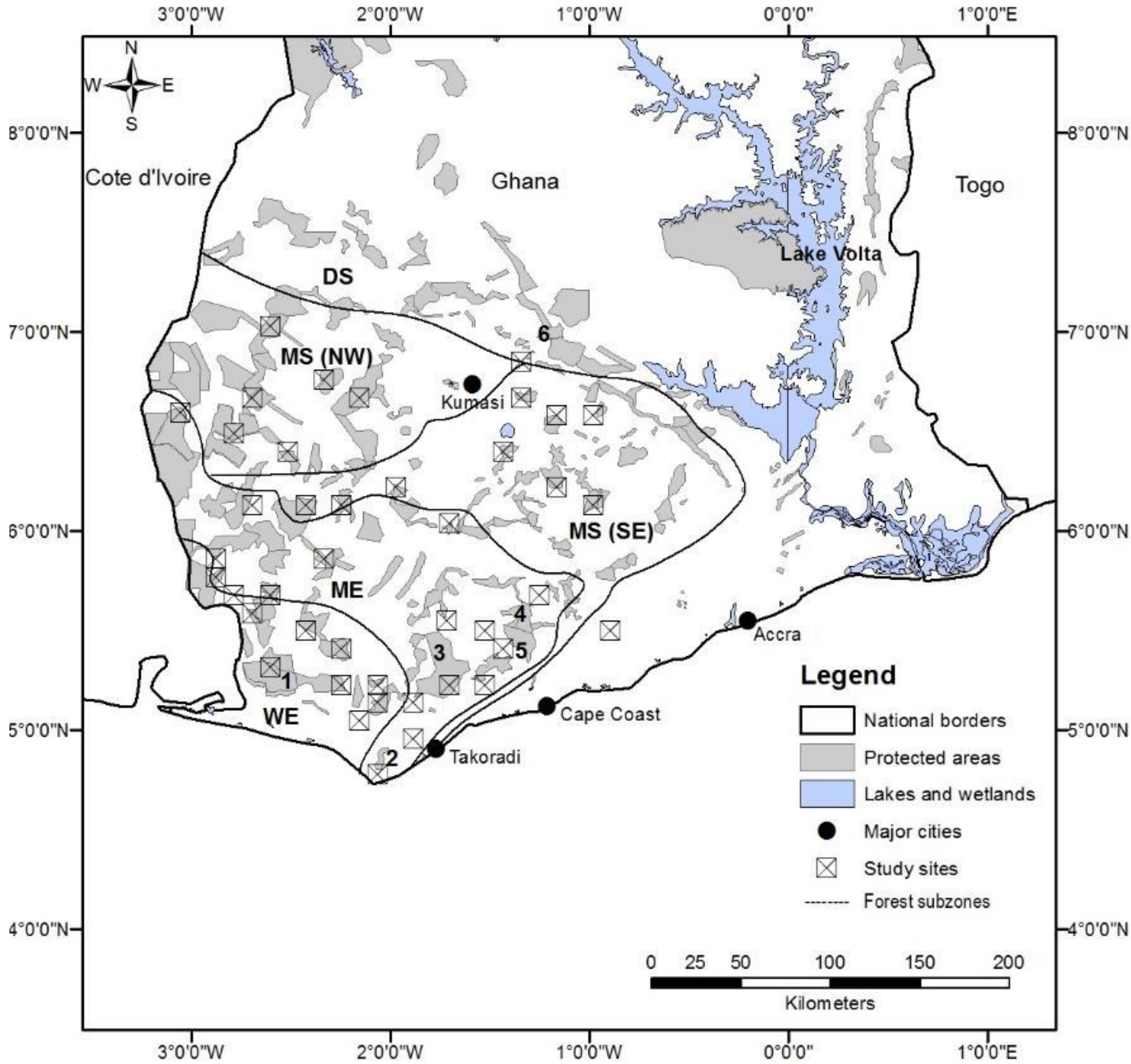

Figure 2.1: Map showing surveyed areas in the high forest zone of southwest Ghana. WE = Wet Evergreen, ME = Moist Evergreen, MS (SE) = Moist Semideciduous (Southeast subtype), MS (NW) = Moist Semideciduous (Northwest subtype), DS = Dry Semideciduous. 1 = Ankasa Game Production Reserve, 2 = Cape Three Points Forest Reserve, 3 = Subri River Forest Reserve, 4 = Assin Attandanso Game Production Reserve, 5 = Kakum National Park and 6 = Bomfobiri Wildlife Sanctuary.

2.3.2 Environmental data

Data for annual rainfall, seasonality of rainfall, human population density and percent forest cover for each site, were obtained using Geographical Information Systems (GIS) techniques. A derived forest disturbance index was also determined for each study site.

Rainfall data for current conditions—interpolations of observed data representative of 1950–2000—were obtained from the WorldClim global climate dataset, which is freely available for ecological modelling (http://www.worldclim.org/). It is a set of global climate layers (climate grids) with a spatial resolution of approximately one square kilometre. The dataset also includes a subset of bioclimatic variables derived from monthly temperature and rainfall values and used to generate more biologically meaningful variables that feed into ecological modelling. Hijmans et al. (1999) gave a detailed account of the methods used to generate the climate layers, and the units and formats of the data. To obtain rainfall estimates for study sites, climate layers for annual rainfall (in mm) and seasonality of rainfall (coefficient of variation) were displayed in ArcMap 10.2.2 and four values were extracted for each environmental variable. The average for the four values for each variable was then used in the ensuing analyses. Similarly, data for human population density estimates (in persons per km^2) were obtained from the Gridded Population of the World, Version 3 (GPWv3) dataset. The dataset is available from the NASA Socioeconomic Data and Applications Centre (SEDAC), which is hosted by the Centre for International Earth Science Information Network (CIESIN) at Columbia University (http://sedac.ciesin.columbia.edu/data/set/gpw-v3-population-density). The data were displayed in ArcMap 10.2.2 and estimates were recorded for eight random points in each study site. The average value for the square was then used for subsequent analyses. To obtain estimates of percent forest cover, a grid of 1 km^2 resolution was laid over each study site using Google Earth and the number of squares filled with forest was expressed as a percentage of the total number of squares in the study site.

The derived forest disturbance index was computed based on four factors: prevalence of hunting, presence or absence of agriculture in forest reserve, level of park protection, and logging history. The index had total values from 3 to 11, with increasing values reflecting higher degree of disturbance. Assigned scores were based on local knowledge of the sites gained during 3–5 day field visits, and through discussions with local land managers. They are as follows:

- Hunting: 1 = low; 2 = medium; 3 = high. Scores were based on comparisons of numbers of spent cartridges, snare traps, encounter rates with hunters and hunter camps and interviews with hunters and opinion leaders.
- Presence or absence of agriculture in forest reserve: 0 = Not observed; 1 = present; 2 = widespread. Present = less than 5 % of the study area; Widespread = 5–25% of the study area
- Level of park protection: 1 = good; 2 = medium; 3 = poor. Scores were determined through a range of evidence including observations of patrols, discussions at park headquarters, interviews with park rangers and managers.
- Logging history: 1 = last logged more than 20 years ago; 2 = 10–20 years ago; 3 = 1–9 years ago. This was ascertained through visits to logging companies, scrutiny of logging maps, physical evidence of recent logging, and interviews with local people. Forests that had no recent history of commercial logging would still no doubt have suffered some kind of felling by local people. These were coded as 1.

2.3.3 Species diversity and abundance

The number of individuals of each species encountered during surveys was collated for each cell and the data tabulated, with species data presented in columns and site data as rows. Species abundance was simply determined as the total number of each species encountered across the general study area over the study period. The Shannon-Wiener diversity index, H (Magurran 2004) was determined for all 42 study sites visited, using version 1.89 of the software PAST (Hammer et al. 2009). However, six sites (230, 567, 680, 682, 729 and 764) for which there were no abundance data (as they were not actually visited) were omitted from analysis.

2.3.4 Canonical correspondence analysis

To decipher the main drivers or environmental gradients influencing frugivorous bird community structure across south-west Ghana, I performed Canonical Correspondence Analysis (ter Braak 1986, 1994, ter Braak and Verdonschot 1995) on the incidence and abundance of bird species at the study sites, using version 3.02a of the software PAST (Hammer et al. 2009). CCA is a multivariate direct gradient ordination technique that, in this case, ordinates bird species or the survey sites at which these species were recorded in relation to environmental axes that are contingent on habitat and physical features (environmental features) recorded at the sites. Essentially, ordination is a research tool for understanding the relationships between biological communities and the environments in which these communities are found. Ordination diagrams, which are graphical outputs of ordinations, are a vital aid in explaining these species-environment relationships (ter Braak 1994).

In the bird incidence (presence/absence) analysis, the ordination was performed for 20 species at all 48 sites involved in this study, including six for which the data were obtained from secondary sources. These were survey reports of Dowsett-Lemaire and Dowsett to the Ghana Wildlife Division of the Forestry Commission of Ghana, Dowsett-Lemaire and Dowsett (2014) and RAP Bulletin of Biological Assessment for a number of study sites (McCullough et al. 2005). However, for the species abundance analysis, the ordination was performed for 19 species (Black-collared Lovebird *Agapornis swindernianus* omitted) at only 42 sites due to the lack of species abundance data for those sites with secondary data sources (also omitted from the Shannon-Wienner diversity analysis). Seven environmental variables were incorporated into the analysis: percentage forest reserve component of each site, derived forest management index, human population density, mean annual rainfall, seasonality of rainfall, Northing, and Easting.

2.4 Results

2.4.1 Incidence, abundance and diversity of frugivorous birds across Ghana

The incidence and abundance of the target bird species varied across study sites (Table 2.1). The Grey Parrot was recorded at ten of the 42 sites surveyed during this study, whereas the Senegal Parrot *Poicephalus senegalus* was recorded only at a single site. However, the African Pied Hornbill *Lophoceros semifasciatus* and the African Green Pigeon *Treron calvus* were recorded at all study sites except 485 where the latter was absent. The most abundant species across the general study area is African Pied Hornbill, followed by African Green Pigeon. The least abundant species include Senegal Parrot, Great Blue Turaco *Corythaeola cristata*, Black-casqued Hornbill *Ceratogymna atrata* and Black Dwarf Hornbill *Tockus hartlaubi*. Of all 42 sites in the current study analysed based on 20 species, site 231 has the highest species richness (12 from 20 species) whereas 141 has the least (2/20). However, historical records from secondary data on six additional sites show that 680 holds the highest richness of 15 species. Site 648 recorded the highest species diversity (Shannon-Wienner index, H = 1.80) followed by site 235 (H = 1.74), whereas site 715 recorded the lowest diversity (H = 0.24, Table 2.1).

Table 2.1: Incidence and abundance of birds in survey squares across Ghana. Data for study sites and 1s with the asterisk (*) symbol are derived from secondary sources and indicate presence-only data. Asterisked presence-only data represent incidence only and do not contribute to abundance. H represents Shannon-Wienner index of species diversity and other column headings representing species names are defined at the bottom of table.

Site no.	Species richness	H	GP	RfP	BnP	AP	WBnP	AGP	BcL	SP	GBT	GT	YbT	WcH	BDH	RbDH	APH	PH	BawcH	BrcH	BlcH	YcH
85	5	1.326		5			4	3					1				13					
140	6	0.716		43				36		1			6	5			370					
141	2	0.653						16									9					
171	3	0.729						33						1			50					
180	4	1.150		71	4			73									42					
202	3	0.773		2				42									25					
208	6	1.244		85				92					15	1		1	138					
214	6	1.51		35		1		27					24	4			32					
230*	14	-	1			1	1	1			1		1	1	1	1	1	1		1	1	1
231	12	1.597	8				1*	31			2		16	1*		2	66	8		1*	4	5
235	8	1.739		7			2	21				1	9	5			27	10				
250	7	1.177			2		3	19					2	1		2	40					
275	4	0.946		4				64						5			53					
297	5	0.98					1	13					3	2			35					
304	5	1.217		42				69					12	1			18					
333	5	0.751		7				58					5	2			205					
343	6	1.539		17	15			27				2	5				33					
358	7	1.581					8	50					44	7		5	22	6				
360	5	1.41						33					16	8			61	55				
368	6	1.044		13				57				1	12	6			156					
388	6	1.288	2					30				2		1			11	23				
406	7	1.584		32		8		54				3	10	6			39					
417	6	1.517	51					60				1	13				68	32				
421	8	1.578	5	2		4		37					20	8			49	3				

422	5	1.091						12				3	9				40	1				
465	7	1.175	2	4				26				1	6	10			79					
483	4	0.601		1				5									51	4				
485	4	0.97	13										2				58	18				
550	10	1.208	11	28			5	92			2	7	42	2		1	321					
554	7	1.095		1				16				2	10	8		4	89					
559	5	0.984		4				24					3	2			56					
567*	8	-	1	1				1			1		1	1			1	1				
614	8	1.508				25		64				22	15	4		2	134	14				
617	4	1.148	7	13				3									25					
648	8	1.801	2	4				28				3	12	9			16	9				
659	5	0.642		14				98				1		8			464					
680*	15	-	1	1				1	1		1	1	1	1		1	1	1	1	1	1	1
682*	5	-				1	1				1				1				1			
694	6	1.402		16		3	9	38						2			39					
696	3	0.298						5						2			92					
715	3	0.235						13									372	7				
729*	9	-		1				1			1	1		1			1	1	1			1
753	10	1.724	2	33			1	26					7	10	3		53	1		9		
764*	5	-						1		1		1					1	1				
757	7	1.280		11	4			54				1	1	8			56					
816	7	1.53		12		4		31					11	6		6	58					
821	6	1.063			2			17				4	1	2			44					
841	4	0.562						3				3		1			41					
Sp. Abundance			**103**	**506**	**27**	**45**	**33**	**1500**		**1**	**4**	**57**	**332**	**137**	**3**	**23**	**3650**	**191**		**9**	**4**	**5**

GP: Grey Parrot; R-fP: Red-fronted Parrot; BnP: Brown-necked Parrot; AP: Afep Pigeon; WB-nP: Western Bronze-naped Pigeon; AGP: African Green Pigeon; B-cL: Black-collared Lovebird; SP: Senegal Parrot; GBT: Great Blue Turaco; GT: Green Turaco; Y-bT: Yellow-billed Turaco; W-cH: White-crested Hornbill; BDH: Black Dwarf Hornbill; R-bDH: Red-billed Dwarf Hornbill; APH: African Pied Hornbill; PH: Piping Hornbill; B-a-w-cH: Black-and-white-casqued Hornbill; Br-cH: Brown-cheeked Hornbill; B-cH: Black-casqued Hornbill; Y-cH: Yellow-casqued Hornbill

2.4.2 Factors influencing frugivore communities across Ghana

Graphical representation of the ordinations of frugivore species' presence/absence and abundance data for the study sites provided some significant insights (Figures 2.2 and 2.3). There was a loose cluster of the large hornbills (60–70 cm, 907–2,100 g; Black-and-white-casqued Hornbill *Bycanistes subcylindricus*, Brown-cheeked, Black-casqued and Yellow-casqued) together with the Black Dwarf Hornbill, Black-collared Lovebird, and Great Blue Turaco. These species had relatively high scores on axis 1, which is itself associated with large areas of reserved forest and high rainfall. On the other hand, some species such as the Red-fronted Parrot, African Green Pigeon, White-crested Hornbill and other widespread species were not particularly associated with any of the axes. Two species, Brown-necked Parrot and Senegal Parrot, were associated with study sites in the north of the general study area. The Grey Parrot and Piping Hornbill, however, appeared to be on their own along the axis of increasing human population density and were not necessarily associated with large areas of reserved forest.

In terms of bird abundance, the ordinations were rather different (Figure 2.3). There was a loose cluster of species, comprising the large hornbills, Great Blue Turaco and Piping Hornbill, which ordinated at high scores on axis 1 (associated with high and seasonal rainfall) and high human population density in the southern parts of the study area (south of the country). The Brown-necked Parrot and Red-fronted Parrot were associated with the north of the study area. Again, the African Green Pigeon, Red-billed Dwarf Hornbill, African Pied Hornbill, White-crested Hornbill did not have high scores on any of the axes.

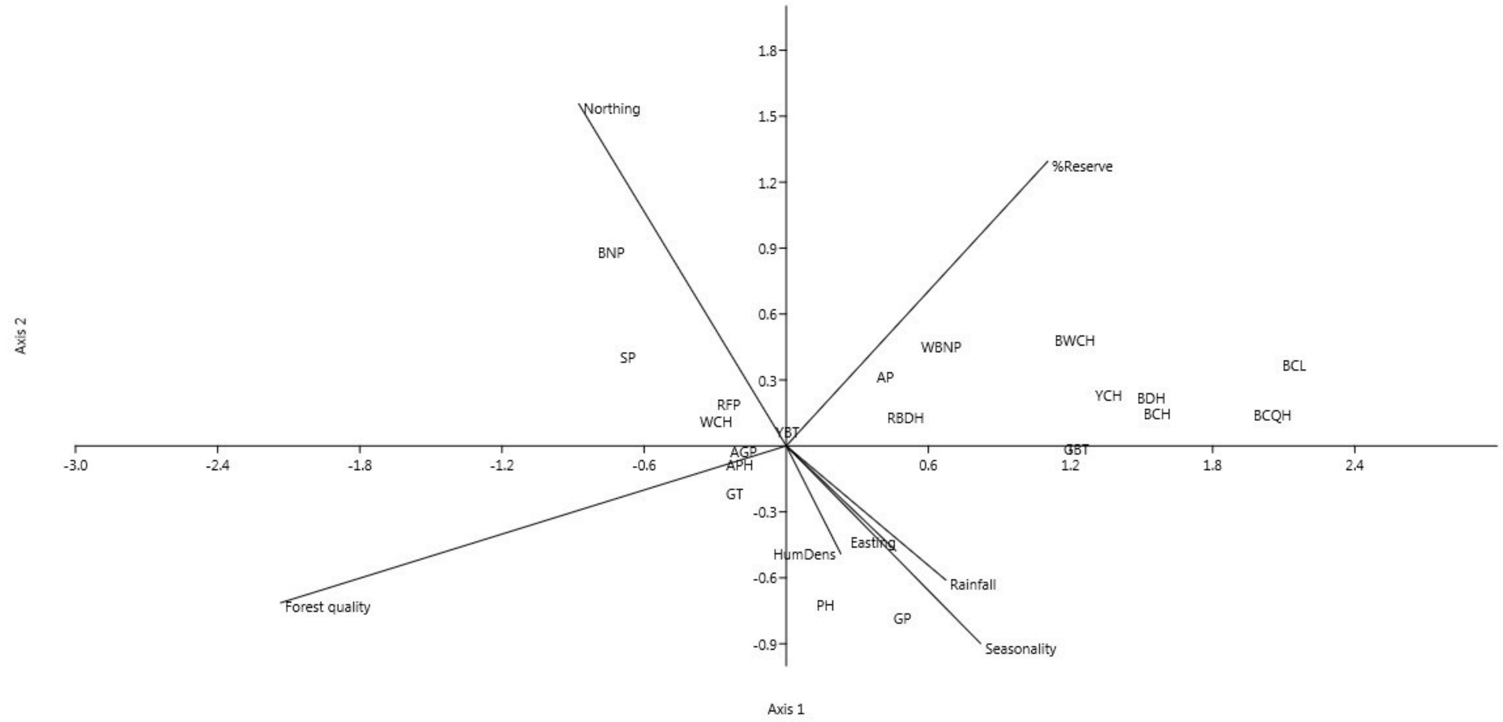

Figure 2.2: Graphical representation of species ordinations based on species presence-absence data from study sites.

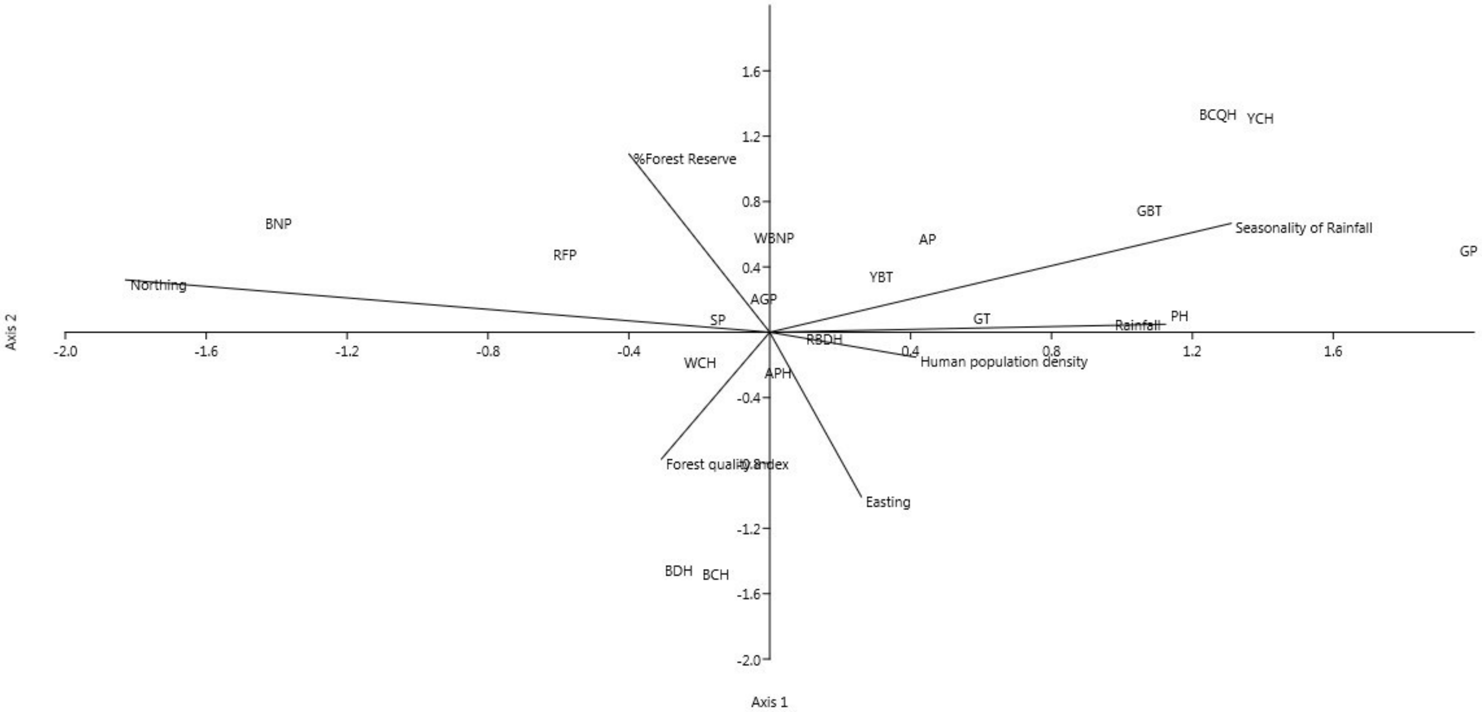

Figure 2.3: Graphical representation of species ordinations based on species abundances at study sites.

2.5 Discussion

Although almost all of Ghana's large frugivores were recorded during the fieldwork, some species were extremely rare and localised. This is exemplified by the fact that in around 150 days of fieldwork in 42 large survey squares (100 km^2), the Grey Parrot was recorded at only ten sites, with 50% (51/103) of individuals recorded (which may have included re-sightings) occurring in a single square. Similarly, merely four Great Blue Turacos were encountered in only two squares, a situation which reflects major population declines and local extirpation from many areas as a direct result of habitat loss and hunting. In their surveys of 28 forest reserves in south-west Ghana (in similar areas to the current study sites) which spanned a period of about one year (June 1995–August 1996) Ntiamoa-Baidu et al. (2000) counted 26 individuals in at least ten reserves. The Black-casqued and Yellow-casqued Hornbills were also recorded at only one site, the Ankasa Resource Reserve (hereafter referred to as Ankasa), which is one of the best-managed protected areas in Ghana with respect to staff patrols and law enforcement (Jachmann 2008, Dowsett-Lemaire and Dowsett 2014). The Brown-cheeked and Black-and-white-casqued Hornbills were never recorded in the surveys. Nonetheless, the Brown-cheeked Hornbill occurs in Ankasa and a few other forest reserves, albeit being rare or extinct in other areas plus not having been previously documented in the transition zone of Ghana (Dowsett-Lemaire and Dowsett 2014). On the other hand, the Black-and-white-casqued Hornbill tends to inhabit dry semi-deciduous and transition-type forest (Dowsett-Lemaire and Dowsett 2014) as it does in Liberia (Gatter 1997). This species, which has very little documentation on its historical distribution in Ghana, is currently confined to Bomfobiri Wildlife Reserve and is approaching extinction in the country (Dowsett-Lemaire and Dowsett 2014). All these large frugivores are threatened with habitat loss and hunting. A few species were very common and widespread, namely the African Pied Hornbill and African Green Pigeon, while the Red-fronted Parrot was relatively widespread but less common. These species are fairly tolerant of forest degradation and fragmentation and may thrive in the absence of heavy hunting or trapping, as a result of their dispersibility, non-territoriality and ability to exploit patchy resources (Lees and Peres 2008, Tobias et al. 2013).

The Grey Parrot was recorded in only ten of the 42 surveyed squares as opposed to being found in at least 20 out of 28 forest reserves nearly two decades ago (Ntiamoa-Baidu et al. 2000). Dändliker (1992), however, saw Grey Parrots in 19 out of 24 roost areas visited just under four years prior to the surveys by Ntiamoa-Baidu et al. (2000). Comparatively, there was therefore a threefold probability of finding the Grey Parrot in the forest zone of Ghana only as recent as two decades ago. The Black-collared Lovebird is, ostensibly, a resident species of the forest zone but may have been missed in our surveys due to its patchy distribution in West Africa in contrast to Eastern and Central Africa (Collar 1997) and extensive local movements in Ghana (Dowsett-Lemaire and Dowsett, 2014). The large hornbills appear to be restricted to south-western Ghana probably both because there are large tracts of fairly good quality forest there, and because they are fairly well protected. Other parts of Ghana also have large forests but habitat degradation and unsustainable hunting appear to be limiting factors. Even though the Red-fronted Parrot is fairly widespread and common it is unrecorded from the wettest areas of south-western Ghana as in Ankasa and Cape Three Points Forest Reserve, where it appears to be allopatric with the Grey Parrot (Holbech 2005, Dowsett-Lemaire and Dowsett 2014).

Most of the frugivores in this study were far too rare to survey using very popular methods such as distance sampling from line transects or point counts (Marsden 1999, McGowan 2001). Encounter rates for my study species were generally extremely low and distance sampling would never work for most, as pooling of data is precluded in this study by habitat heterogeneity and differences in detectability and the fact that the majority of records were of birds in flight (Marsden 1999, Buckland et al. 2008). Generally, about 60 or more perched records of each species are needed to generate reliable density estimates (Bibby et al. 1998, Buckland et al. 2001, 2008), although as low as 40–50 yielded reliable parrot density estimates in New Caledonia (Legault et al. 2013). Marsden (1999) found that several hundred point counts would be needed to produce reasonable density estimates for various species of parrots and hornbills in Indonesia – and these birds are considerably commoner than most of the species in the present study. The fact that only just over 100 Grey Parrots were recorded in Ghana in over 18 months of fieldwork, with 52 records taken at nine sites and not a single bird at 32 other sites, indicates that the species has become extremely rare in the country. My survey methods, which were similar to those of Clemmons' (2003) in Guinea and Guinea Bissau, allowed large areas to be covered in an attempt to maximise the potential of seeing birds, but it was not possible to determine actual population densities due to inadequate number of sightings, just as in her study. In Guinea and Ghana, respectively, Dändliker (1992) used long-distance travels by vehicle in search of Grey Parrot roosts informed by prior and on-site information, resulting in counts at roosts and of parrots to and from supposed roosts. Various studies have been conducted in Cameroon that employed the line transect method (Tamungang 1998) and point count method (Tamungang and Cheke 2012, Tamungang et al. 2013, Tamungang et al. 2014) for determining species densities and abundance. These methods are, however, not useful in Ghana owing to the high degree of rarity of Grey Parrots and many other frugivores. Similarly, McGowan's (2001) method of searching for Grey Parrot nests in Nigeria may not necessarily be applicable to Ghana, as it currently seems there are no professional full-time trappers to be recruited for such intensive nest searches; in any case, such searches would invariably yield negligible success rates. Furthermore, only very small areas can be assessed by this approach, which is incongruent with our objective of covering very large areas of potential Grey Parrot and other frugivore habitat in our study. CCA does, however, allow an analysis of the frugivore community make-up of different areas, of which species co-occur, and of the broad environmental factors that influence community make-up.

The ordination illustrated some important clusters of frugivore species. The large hornbills and Great Blue Turaco were loosely grouped together, and their presence was strongly correlated with large areas of reserved forest within study squares and with minimal levels of forest disturbance. This finding may be explained by the fact that large frugivorous birds such as hornbills have been major targets of hunters after the extirpation of traditional meat sources such as primates and ungulates (Holbech 1998, 2014, Waltert et al. 2010), and have subsequently become restricted to the large and well-protected forests (Jachmann 2008) of south-west Ghana. In a similar study of large frugivorous birds on the island of Luzon in the Philippines, Española et al. (2013) concluded that frugivore community structure has largely been shaped by anthropogenic factors in spite of natural biogeographical process. Very widespread species such as the Yellow-billed Turaco, African Green Pigeon and African Pied and White-crested Hornbills, in addition to the Red-fronted Parrot and Green Turaco, were not influenced by any environmental variable. These species are amongst those found to be very widespread and common by Ntiamoa-Baidu et al. (2000) during surveys that covered the southern part of Ghana in the mid-1990s. The Brown-necked Parrot is predominantly a transition-zone forest species, but also inhabits areas further south and deep into the rainforests of south-west Ghana. However Senegal Parrot is, found in both the transition and savanna zones of Ghana (Dowsett-Lemaire and Dowsett 2014). This explains why the two species are depicted as 'northing', as they were both recorded in habitats to the north of the survey area. The Grey Parrot and Piping Hornbill were often found in anthropogenic landscapes during this study. Although Bennun et al. (1996) classified the Grey Parrot as a forest-dependent species in Kenya and Uganda, the species easily passes for a forest generalist. This is because accounts of historical occurrence based on interviews with several hundred rural dwellers (data to be analysed separately) indicate that it was not uncommon to find the species breeding in farmland with remnant trees, and near human settlement (Twanza and Pomeroy 2011, Irumba 2013). Dändliker (1992) often found major roosts on oil palm and coconut palm plantations in Ghana, although these roosts were usually close or adjacent to major forest reserves. McGowan (2001) also reported of a roost located next to a village with potential peak counts of up to 2,000 Grey Parrots. The ordination indicates that Grey Parrots are also linked to areas with high rainfall and rainfall seasonality, two variables which appear to be closely correlated.

2.6 Conservation implications

Most large avian frugivores in Ghana are not common and widely distributed. There are exceptions, such as African Green Pigeon and African Pied Hornbill, but species such as the large hornbills and the Great Blue Turaco are thought to be present in few regions of Ghana due to range contractions resulting from habitat loss and hunting (this study, Dowsett-Lemaire and Dowsett 2014). The absence of large species from many areas may mean that seed dispersal could be compromised in these forests. Studies elsewhere have found that the collapse of populations of groups of seed-dispersers in forest reserves could trigger negative consequences for the structure and functioning of the reserves (Higman et al. 1999, Sodhi et al. 2008, Kitamura 2011). Nonetheless, few studies have evaluated long-term alterations in tree population dynamics or community structure as a result of reduced seed dispersal, and those that have, including Terborgh et al. (2008) and Harrison et al. (2013), have produced contradictory findings.

The diets of the large hornbills in Ghana may include Raffia palms *Raphia spp*. and Oil Palm *Elaeis guineensis*, as well as the fruits and/or seeds of some tree species of the family Myristicaceae, but the full range of dietary materials are certainly not known (Dowsett-Lemaire and Dowsett 2014). It is not known for certain why these species are absent from many areas, but hunting is rife and undoubtedly a plausible cause. Also, the lack of nest holes due to the extraction of very large trees from selectively logged forest reserves is a potential problem (Marsden and Jones 1997, Marsden et al. 2001, Marsden and Pilgrim 2003).

To prevent the inevitable extinction of many of these large frugivores in the long term, conservation efforts must inevitably be focused on forest reserves with remnant populations e.g. Ankasa Resource Rserve, Cape Three Point Forest Reserve, Kakum National Park and Subri River Forest eserve. Active conservation education in satellite communities of protected areas coupled with enhanced protection by way of increased reserve patrols are a good starting point. Changing logging practices to leave very big old trees with nest holes is highly recommended, as such trees are essential to the maintenance of cavity nesters (Dickson et al. 1983) such as hornbills and parrots. The likelihood of competition for nest holes between the very common African Pied Hornbill and other species has not been investigated in Ghana, but agonistic interactions have previously been recorded between hornbills and other cavity nesters (Fotso 1996, Clemmons 2003, Maheswaran and Balasubramanian 2003).

The next chapter will perform an anlysis and synthesis of habitat associations and distribution of avian frugivores using species distribution models (Maxent) to map the occupancy of Ghana's frugivores.

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Chapter 3

DISTRIBUTION MODELLING FOR LARGE AVIAN FRUGIVORES ACROSS GHANA

3.1 Abstract

Large avian frugivores are important both for biodiversity conservation and as ecosystem service providers. However, many species have declined across much of West Africa. I used Maxent, a presence-only species distribution modelling technique, to predict the distribution and probability of occurrence of 15 species of parrot, hornbill, pigeon and turaco across Ghana, based on environmental variables including land cover types, enhanced vegetation index, net primary productivity, human population density and climate data. The Maxent models were run with a combination of default and alternative settings. To enable an assessment of model robustness for each species, 20 replicate runs were performed on the data with 75% of the presence records selected randomly for model training, and the remainder for model testing. Frugivores showed varying degrees of being tied to Ghana's large forest reserves, with Afep Pigeon, Western Bronze-naped Pigeon, Great Blue Turaco, Yellow-billed Turaco, Black Dwarf Hornbill and Red-billed Dwarf Hornbill being most strongly restricted. In contrast, African Green Pigeon, Brown-necked Parrot and African Pied Hornbill had their predicted distributions spread across the wider landscape. Most species had higher probability of occurrence in the southwest of the country. The main driver of distribution in the majority of species was land cover type (11/15 species), with forest habitats preferred in 90% of cases as opposed to shrub land, cropland and urban built-up areas. Differences in human population density and enhanced vegetation index were not important for most species. Key sites for conservation of the Ghana's large avian

frugivores are the large forest reserves in the southwest of the country. It is crucial that Ghana's forest reserves are adequately protected to ensure that human encroachment and logging are controlled.

3.2 Introduction

3.2.1 Types and distribution of frugivores in Ghana

The ecology, taxonomy and global geographical distributions of birds are far better known than in comparable groups of animals (Schulze et al. 2004, Gray et al. 2007, BirdLife International 2012a). Birds are of great importance to general ecological processes (Sekercioglu 2006, Whelan et al. 2015), and frugivores, especially, perform vital ecosystem services that include the maintenance of forest structure (Cordeiro and Howe 2001, Sodhi et al. 2008, Kankam and Oduro 2012). For example, many forest-inhabiting hornbills are important seed dispersers (Whitney et al. 1998, Whitney and Smith 1998, Holbrook and Smith 2000, Kinnaird and O'Brien 2007). Aside from dispersal, many frugivores facilitate the germination of fruit seeds by removal of skin and pulp, as many seeds fail to germinate from intact fruits (Samuels and Levey 2005). Furthermore, frugivores are also functionally important in several ways: they mediate the escape of seeds from seed predators through dispersal, improve seed germination through digestive processes, increase economic yield from farm produce, and increase gene-flow through seed dispersal and pollination (Sekercioglu et al. 2004, Sekercioglu 2006).

Ghana is rich in avian frugivores, having a high diversity of parrots (7 species), turacos (5), hornbills (12, with small to medium-sized species mainly omnivorous) as well as two exclusively frugivorous species among 17 pigeons (Baptista et al. 1997). Among these frugivores two species of hornbill, Brown-cheeked *Bycanistes cylindricus* and Yellow-casqued *Ceratogymna elata*, as well as the Grey Parrot *Psittacus erithacus*, are listed as 'Vulnerable' according to the IUCN Red List scheme. The main threats to these species appear to be forest fragmentation and loss, and exploitation for food and/or the pet trade (BirdLife International 2008a, 2008b, 2012b, 2013; Dowsett-Lemaire and Dowsett 2014). The majority of these avian frugivores are thought to be predominantly forest-dwelling (Table 3.1), but others inhabit a variety of habitats including thickets and farmbush. The distribution of these species have been documented over Ghana using a 50km × 50km grid (Dowsett-Lemaire and Dowsett 2014). However, many species' populations and distributions appear to have declined, probably owing to hunting, habitat change and/or modification (Dowsett-Lemaire and Dowsett 2014).

In the last 50 years alone, Ghana lost some 90% of its forest cover (http://rainforests.mongabay.com/20ghana.htm). Logging and farming are major causes of deforestation and forest habitat alteration in the country, compounded by poor forest management strategy, fire, mining and quarrying (Benhin and Barbier 2004). Annual deforestation in Ghana has been estimated at 650 km^2 (World Bank 2007) and continues to escalate (Marfo 2010). This trend of forest loss puts the country's biodiversity at risk, and has potential detrimental consequences for frugivores.

3.2.2 Species distribution modelling

Species distribution models (SDMs) are quantitative methods which associate the occurrence of a species at multiple locations with environmental variables to predict distributions based on estimates of the suitability of sites where the species is likely to occur (Wisz et al. 2008, Elith and Leathwick 2009, Duan et al. 2014, Guillera-Arroita et al. 2015). SDMs are a fast-growing field of research (Brotons 2014), and have variously been referred to, *inter alia*, as ecological niche modelling, climate envelope modelling and habitat suitability modelling (Duan et al. 2014). SDM techniques have been applied extensively in various disciplines such as ecology, biogeography, biodiversity conservation and natural resource management (Guisan and Thuiller 2005, Newbold 2010, Franklin 2013, Guisan et al. 2013) specifically for the management of threatened species, effects of climate change on species distributions, studies on phylogeographic patterns and the management of landscapes (Guillera-Arroita et al. 2015).

There is, however, an array of modelling techniques available (Phillips et al. 2004, Segurado and Araújo 2004, Elith et al. 2006, Guillera-Arroita et al. 2015). These can be grouped into two major categories based on the type of species occurrence data used (Elith et al. 2011, Guillera-Arroita et al. 2015). Some, including Environmental Niche Factor Analysis (ENFA), Multivariate Adaptive Regression Splines (MARS), Genetic Algorithm for Ruleset Prediction (GARP), and Maximum Entropy (MAXENT), use presence–background data (often referred to as presence–only data). Others, such as Generalized Linear Models (GLMs) and Generalized Additive Models (GAMs) — treated *sensu lato* by some authors as SDMs — use presence–absence data (see Segurado and Araújo 2004, Elith et al. 2006, 2011).

In the recent past, SDM techniques predominantly applied presence–absence data for predictions. However, the increasing availability of electronic forms of presence–only data coupled with the plethora of environmental data from Geographical Information Systems (GIS) has resulted in a major paradigm shift in favour of presence–only approaches (Elith et al. 2006, Phillips and Dudík 2008, Elith et al. 2011). Presence–only techniques have become popular for two main reasons. First, there are huge open–access datasets of presence–only records, whereas absence data are often unavailable. Second, absence data are often unreliable even when available e.g. owing to inadequate sampling effort that could result in pseudo-absences, especially in regions of high biodiversity (Anderson et al. 2003, Phillips et al. 2006, Anderson 2012).

Among the many SDM techniques currently available, Maxent is widely used owing to its efficacy and versatility in predicting species distributions (Elith et al. 2006, Heikkinen et al. 2006, Hernandez et al. 2006, Wisz et al. 2008, Warren and Seifert 2011). Phillips et al. (2006) described it as a general–purpose method for making deductions based on incomplete information. Maxent applies the principle of maximum entropy (Jaynes 1957a, b) to presence–only data to evaluate a set of functions that relate environmental predictors to habitat suitability as a means of determining the potential geographic distribution of a species (Phillips et al. 2006, Warren and Seifert 2011). The principle states that, subject to precisely stated prior data, the probability distribution that best represents the current state of knowledge is the one with largest entropy. An inherent assumption of the programme is that species without ecological barriers disperse uniformly (Duan et al. 2014).

3.2.3 Aim and objectives

The aims of this chapter are to identify likely areas of occupancy (AOO) for the large frugivorous birds of Ghana, the strongest environmental predictors of their current distributions, and, ultimately the most important areas for focused conservation action. To achieve these aims, I addressed the following objectives:

1. To use presence-only species distribution models to map the probability of occurrence of 15 species across Ghana, using environmental variables including land cover types, EVI, NPP, human population density and climatic data.
2. To use response curves for each species with individual environmental variables to determine the strongest drivers/correlates of current distribution.

3. To identify hotspots for frugivore conservation and to guide conservation actions onto appropriate locations.

3.3 Methods

3.3.1 Study area and bird data acquisition

Current georeferenced presence locations—defined here as GPS locations of bird presence records between 2010 and 2014—were obtained from the high forest zone (HFZ) of Ghana for 15 avian frugivores (Table 3.1) through roost and transect surveys conducted throughout the southwest of the country between April 2012 and June 2014 (Figure 3.1). The HFZ was partitioned into a grid of 100-km^2 cells and a sample of 42 cells was selected, not randomly, but to maximise the likelihood of encountering frugivore populations (Figure 3.1). This approach was based on the presence of substantial forest cover. Each cell was visited for periods of 3–5 days, with surveys conducted on each day between 05h45 and 11h00. Surveys were conducted by walking along hunter or farmer footpaths and along drivable pathways connecting villages or towns. Survey routes were walked in the company of a local guide, and all individual birds heard or seen along the route, perched or in flight, were recorded together with direction of flight. Furthermore, long watches were conducted from vantage points between 16h00 and 18h00 on some days, timed to correspond with the periods of afternoon flight towards roosts. The diversity of habitat types surveyed included forest reserves containing primary and secondary forest (most forest reserves have been selectively logged), mosaics of old fallow and degraded forest remnants, small-scale agro-ecosystems, surrounding habitats of rural settlements. Other habitats surveyed were large-scale oil palm *Elaeis guineensis* and cocoa *Theobroma cacao* plantations, as well as swampy areas characterised by bamboo *Bambusa spp*. and raffia palms *Raphia spp*.

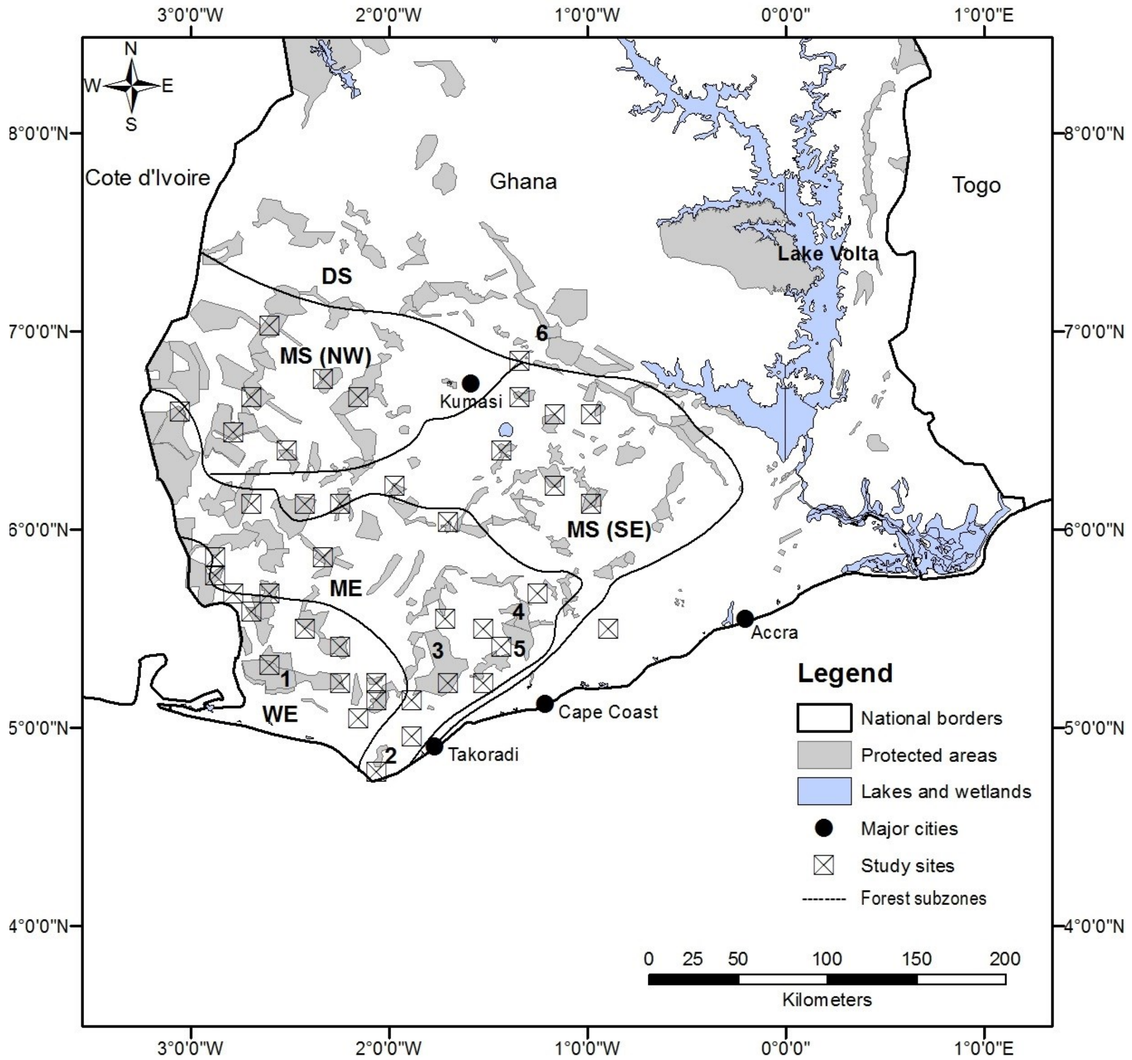


Figure 3.1: Map showing surveyed areas in the high forest zone of southwest Ghana. WE = Wet Evergreen, ME = Moist Evergreen, MS (SE) = Moist Semideciduous (Southeast subtype), MS (NW) = Moist Semideciduous (Northwest subtype), DS = Dry Semideciduous. 1 = Ankasa Game Production Reserve, 2 = Cape Three Points Forest Reserve, 3 = Subri River Forest Reserve, 4 = Assin Attandanso Game Production Reserve, 5 = Kakum National Park and 6 = Bomfobiri Wildlife Sanctuary.

Additional bird presence records were collated from the Global Biodiversity Information Facility (GBIF, http://www.gbif.org/). The GBIF is an internet-based international open data resource that enables access to data about species globally (e.g.

Di Febbraro et al. 2013, Faulkner et al. 2014, Ficetola et al. 2015). The GBIF dataset increased not only the total number of records available for modelling but also, more importantly, the total geographical coverage of the sampled area (Figure 3.2). The facility's data derives from over three centuries of natural history exploration and includes current observations from citizen scientists, researchers and automated monitoring programmes.

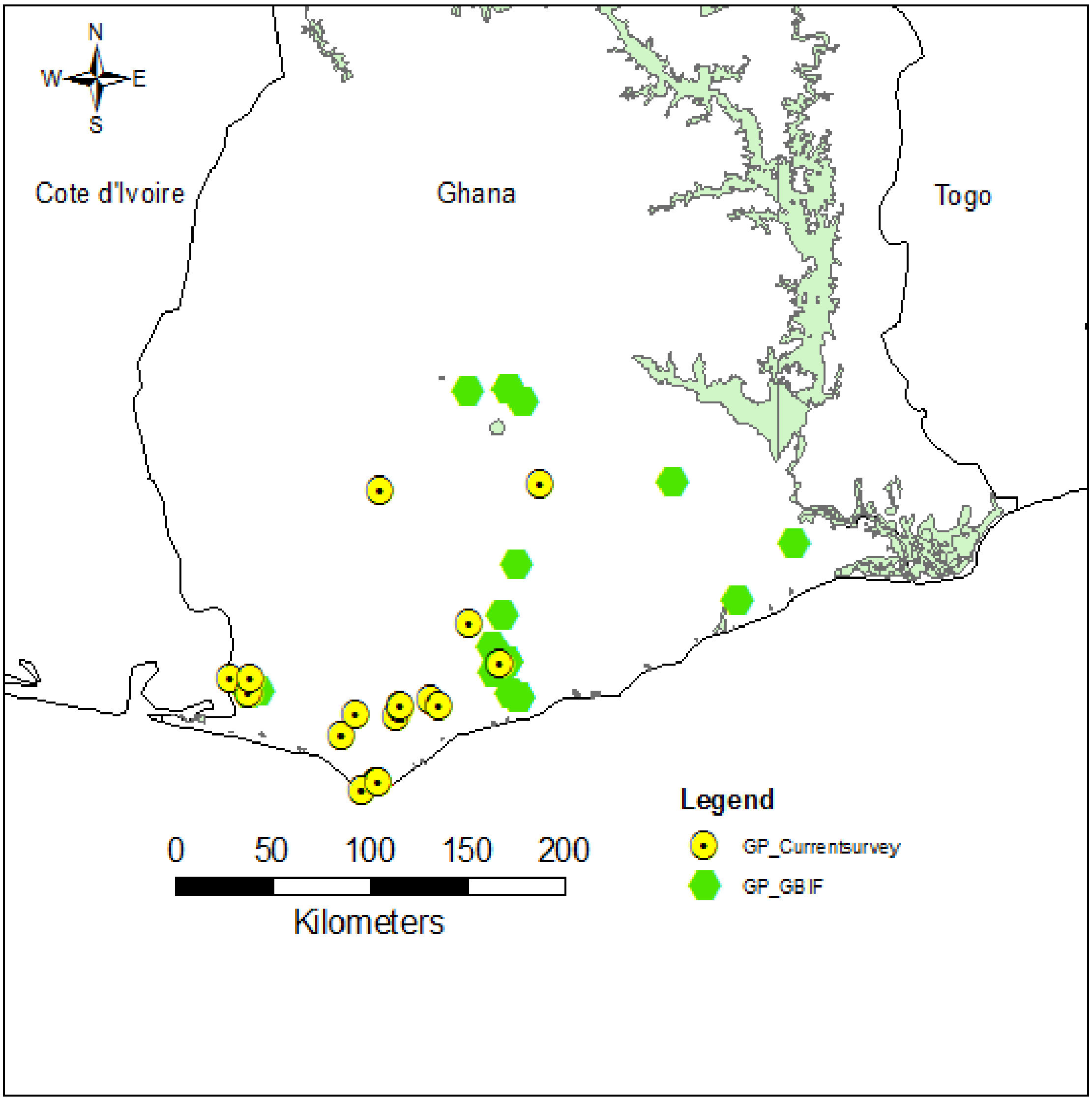


Figure 3.2: Map showing species presence points for Grey Parrot (GP). Note the contribution of GBIF data to spatial coverage of presence points.

It serves as a single access node to hundreds of thousands of species records shared by hundreds of institutions globally, and is cited by over 1400 peer-reviewed research publications as a source of data (http://www.gbif.org/what-is-gbif). The GBIF database is useful because it increased the total dataset for analyses, saved time and cost that would have been incurred to conduct further surveys, and was in a ready-to-use format that required minimal manipulation. The database, however, contains appreciable amounts of erroneous data points and downloaded datasets often require some data cleansing prior to use (e.g. Maldonado et al. 2015).

Table 3.1: Species names and number of presence records input into Maxent for model development.

Species		No. of presence records		
Common name	Scientific name	This study	GBIF	Total
Grey Parrot	*Psittacus erithacus*	19	41	60
Red-fronted Parrot	*Poicephalus gulielmi*	184	77	261
Brown-necked Parrot	*Poicephalus robustus*	12	14	26
African Green Pigeon	*Treron calvus*	483	277	760
Afep Pigeon	*Columba unicincta*	19	12	31
Western Bronze-naped Pigeon	*Columba iriditorques*	24	15	39
Great Blue Turaco	*Corythaeola cristata*	4	30	34
Yellow-billed Turaco	*Tauraco macrorhynchus*	212	132	344
Green Turaco	*Tauraco persa*	40	47	87
African Pied Hornbill	*Tockus fasciatus*	801	317	1,118
White-crested Hornbill	*Tockus albocristatus*	103	72	175
Piping Hornbill	*Ceratogymna fistulator*	67	92	159
Black Dwarf Hornbill	*Tockus hartlaubi*	2	31	33
Red-billed Dwarf Hornbill	*Tockus camurus*	13	21	34
Yellow-casqued Hornbill	*Ceratogymna elata*	3	17	20
Total		1,987	1,215	3,181

Together with field data from this study, nearly 3,200 records were available for developing SDMs for the 15 species. However, to generate model predictions that reflect current distributions of avian frugivores in Ghana, presence records from GBIF were filtered to exclude all sightings predating the year 2010. Duplicate records from a single cell were also removed. Using these criteria, the combined number of records from both the present study and the GBIF dataset selected for modelling was reduced to 3,181 (maximum = 1,118, mean = 212.1 and min = 20; Table 3.1).

3.3.2 Environmental variables

Seven environmental variables were selected for model development owing to their ecological relevance to the modelled species (see Elith et al. 2006, Phillips et al. 2006, Gonzalez et al. 2011, Fourcade et al. 2014). A small number of variables was used to minimise over-parameterisation and to ensure high levels of model accuracy (Warren and Seifert 2011, Novaes e Silva et al. 2014). Sources and formats of the seven data layers are given in Table 3.2. Estimates of annual rainfall and its seasonality were extracted from the WorldClim-Global Climate Data, which are freely available for ecological modelling (http://www.worldclim.org/). This is a set of global climate layers (climate grids) with a spatial resolution (pixel size) of approximately one square kilometre (Hijmans et al. 2005). Percentage tree cover, land cover types, enhanced vegetation index (EVI), and net primary productivity (NPP) were obtained from the MODIS website (https://lpdaac.usgs.gov). The percent tree cover data layer—also called vegetation continuous fields (VCF)—provides a quantitative representation of ground cover with enhanced spatial detail, and is useful for identifying forested areas for environmental modelling (Townshend et al. 2011). A categorical data layer of four vegetation classes (see Table 3.2) was reclassified from the 17-class International

Geosphere-Biosphere Programme classification system (IGBP, Loveland and Belward 1997, Friedl et al. 2010). EVI minimises canopy background variations and maintains sensitivity over dense vegetation conditions, and thus was used instead of NDVI (Normalised Difference Vegetation Index). EVI also removes residual atmosphere contamination caused by smoke and sub-pixel thin clouds (Solano et al. 2010). NPP is a measure of the rate at which all plants in an ecosystem produce net useful energy, and in itself can be a measure of habitat suitability (Heinsch et al. 2003). Similarly, data for human population density estimates in persons per square kilometre were obtained from the Gridded Population of the World, Version 4 (GPWv4) dataset (http://www.ciesin.columbia.edu/data/gpw-v4/). All data layers were manipulated and formatted in ArcMap 10.2.2 to yield datasets of same projection, spatial extent, grid cell size, and alignment consistent with the requirements of Maxent software (Phillips undated, Elith et al. 2006).

Table 3.2: Environmental variables used for model construction. #: VCF and land cover types originally had resolutions of 0.25 and 0.50 km^2, respectively, but were both converted to 1 km^2 pixels. *: Land cover types were put into four categories as follow: 1 = evergreen + deciduous forest, 2 = open + closed shrubland, 3 = cropland + natural vegetation and cropland, and 4 = urban + built-up area.

Variable	Source and detailed description
Climate	http://worldclim.org
Annual rainfall (BIO12)	Hijmans et al. 2005
Seasonality of rainfall (BIO15)	
Habitat	https://lpdaac.usgs.gov
Percentage tree cover (VCF)#	Townsend et al. 2011
Land cover types#*	Friedl et al. 2010
Enhanced vegetation index	Solano et al. 2010
Net primary productivity	Heinsch et al. 2003
Anthropogenic	http://www.ciesin.columbia.edu/data/gpw-v4/
Human population density	

3.3.3 Model development and evaluation

Version 3.3.3k of the Maxent software (http://www.cs.princeton.edu/~schapire/maxent/) was used to develop the SDMs for the 15 frugivorous bird species. The choice of a presence-only analytical approach was made for two reasons. First, some of the study species are nomadic within the forest zone in response to the availability of food resources (e.g. parrots and hornbills, Dändliker 1992, Dowsett-Lemaire and Dowsett 2014), and their absence in surveyed sites did not necessarily imply unsuitability of such sites as potential habitat. Second, some species have suffered drastic population declines (Dowsett-Lemaire and Dowsett 2014, Martin et al. 2014, Marsden et al. 2015) and hence may not be occupying all their potential habitats (Cianfrani et al. 2010). Absence from surveyed sites may therefore, be related to other factors other than habitat relationships (Geary et al. 2013).

Following contemporary trends in the application of Maxent, with cues from recent findings (e.g. Merow et al. 2013, Elith et al. 2011), the models were run with a combination of default and alternative settings. To enable an assessment of model robustness for each species, 20 replicate runs were performed on the data with 75% of the presence records selected randomly for model training, and the remainder for the model. The subsample replication option was selected, with a maximum of 5,000 iterations per replicate run, 10,000 maximum background points, and a convergence threshold of 0.00001. Even though some authors have proposed the application of species-specific values for model regularisation (e.g. Anderson and Gonzalez 2011, Warren and Seifert 2011), the default value of 1 is adequately suitable for most presence-only datasets (Phillips et al. 2004, Phillips and Dudik 2008) and is still widely used (e.g. Abolafya et al. 2013). To minimise the effects of sampling bias, Maxent was instructed to apply one presence record per cell by activating the 'remove duplicate presence records' tab.

To evaluate the performance of the model for each species, the receiver operating characteristic (ROC) was used. This approach assesses the performance of a Maxent model using the area under the ROC curve (AUC), and is a widely used measure of model performance (Elith et al. 2006, Wisz et al. 2008, Vidal-Garcia and Serio-Silva 2011). The AUC represents the probability of ranking a presence locality above a background locality (pseudo-absence) when both are chosen at random (Phillips et al. 2006, Phillip and Dudik 2008). Models with AUC values of 0.5 indicate a prediction no better than random whereas a value of 1 is a perfect prediction (Elith et al. 2006, Phillips and Dudik 2008, Abolafya et al. 2013). The contribution of each environmental variable to models was assessed by performing a jackknife test in Maxent, which determines the influence of each variable on model gain by excluding it or applying that variable alone in analyses (Elith et al. 2006, Vidal-Garcia and Serio-Silva 2011).

3.4 Results

3.4.1 Model performance

The AUC values for the predicted distributions of all 15 avian frugivores were markedly higher than would be random predictions (range = 0.72–0.94; Table 3.3). Distribution models for six species predicted very high probabilities of occurrence (PoOs), with their AUC values ranging from 0.90–0.94 (Table 3.3). All other species except the Brown-necked Parrot (AUC = 0.72) had AUCs greater than 0.80. The average AUC across all species was 0.87. There was no significant correlation between numbers of species presence records and mean AUC for the species (r_s = - 0.17, n = 15, p = 0.54).

Table 3.3: Number of presence records actually used in the Maxent models and mean AUC values with standard deviation for each species. AUC values are arranged in decreasing order for easy assessment.

Species	No. of records	AUC (mean ± SD)
Yellow-casqued Hornbill	8	0.94 ± 0.03
Yellow-billed Turaco	136	0.94 ± 0.01
Western Bronze-naped Pigeon	25	0.92 ± 0.04
Great Blue Turaco	12	0.91 ± 0.05
Red-billed Dwarf Hornbill	22	0.90 ± 0.04
Piping Hornbill	81	0.90 ± 0.04
Red-fronted Parrot	143	0.89 ± 0.02
White-crested Hornbill	110	0.88 ± 0.02
Grey Parrot	33	0.86 ± 0.06
Afep Pigeon	17	0.85 ± 0.05
African Green Pigeon	320	0.84 ± 0.02
Black Dwarf Hornbill	13	0.83 ± 0.05
African Pied Hornbill	511	0.82 ± 0.02
Green Turaco	46	0.81 ± 0.07
Brown-necked Parrot	14	0.72 ± 0.09

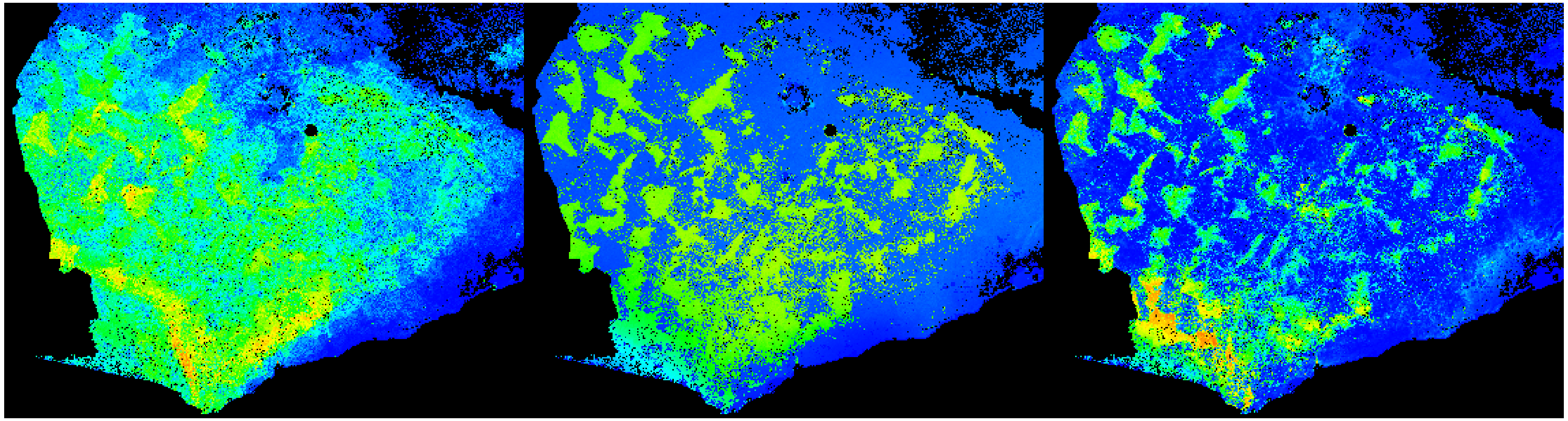
3.4.2 Predicted probabilities of species occurrence

The predicted distribution of some species is spread across much of the forest zone whereas it is much patchier for others (Figure 3.3). African Green Pigeon, Brown-necked Parrot, African Pied Hornbill and Green Turaco show relatively high and even probabilities of occurrence (PoOs) right across the landscape of southwestern Ghana as compared to the other species. However, there are areas for each of these species which have comparatively higher or lower PoOs. Three of the four species (African Green Pigeon, Brown-necked Parrot, African Pied Hornbill) are largely predicted to be absent from the coastal ecological zones, namely Coastal Scrub and Grassland, and Strand and

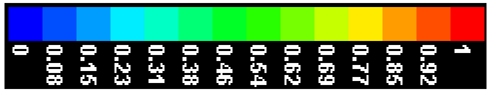
Mangrove vegetation (shrubby coastal vegetation). They are also predicted to be largely absent (perhaps African Pied Hornbill is an exception) within the heavily degraded urban and peri-urban areas of Kumasi. There appear to be areas of higher PoOs for African Green Pigeon, Green Turaco and African Pied Hornbill around Subri River Forest Reserve and Kakum National Park, and for African Green Pigeon and African Pied Hornbill, respectively, along the ecotone between the Wet Evergreen and Moist Evergreen vegetation zones.

The remaining species show variation in the degree to which their PoO is predicted to be centred in the wet southwest. Piping Hornbill, Red-billed Dwarf Hornbill, Yellow-casqued Hornbill, and especially, Great Blue Turaco, have relatively high PoOs in the southwest around Ankasa and Draw River Forest Reserves. The PoO of Piping Hornbill is slightly different in that the centres of its highest PoO are around Draw River, Ndumfri, Nueng, Cape Three Points and Subri River FRs. Great Blue Turaco shows the strongest focus in the Wet Evergreen forest zone, with very low probabilities anywhere else in the country. The predicted PoO of Yellow-billed Turaco appears to be the reverse of that of the Great Blue Turaco, with the latter replacing the former in the extreme southwest, and with an area of overlap further east. Yellow-billed Turaco, although certainly not ubiquitous across Ghana, is predicted to be more widespread than Great Blue Turaco, whose predicted distribution is more restricted to Ghana's largest forests. A similar pattern, although not as distinct was Red-fronted Parrot 'replacing' Grey Parrot away from the extreme south and southwest.

An important pattern shared by some species is for their predicted distribution in the north of the HFZ, and perhaps east, to be very strongly delineated by the presence of large forest reserves. This delineation, however, is not so obvious in the southwest, where areas outside of protected areas are presumably more suitable than they are in the north. Species that show this pattern to a greater or lesser degree are pigeons, Afep Pigeon, Western Bronze-naped Pigeon and Black Dwarf Hornbill. A few species, namely the Grey Parrot, Great Blue Turaco, Piping Hornbill and Yellow-casqued Hornbill, have very low PoOs east of the forest zone compared to the southwest, with a similar situation occurring in the north with respect to Great Blue Turaco, Piping Hornbill and Yellow-casqued Hornbill. It is also noteworthy that although African Green Pigeon, Brown-necked Parrot and African Pied Hornbill have focal areas with high PoOs, they also show a ubiquitous distribution over the forest zone.

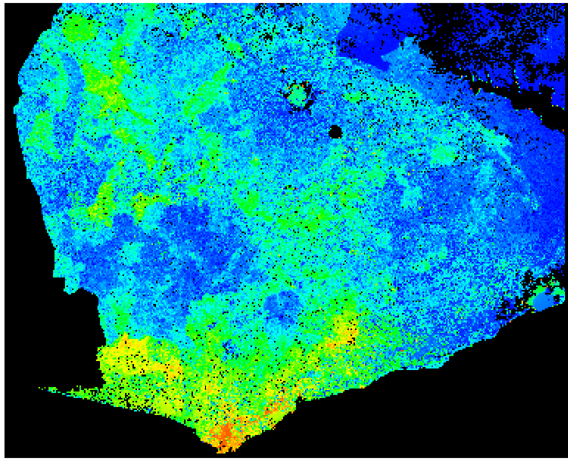


African Green Pigeon | Afep Pigeon | Western Bronze-naped Pigeon

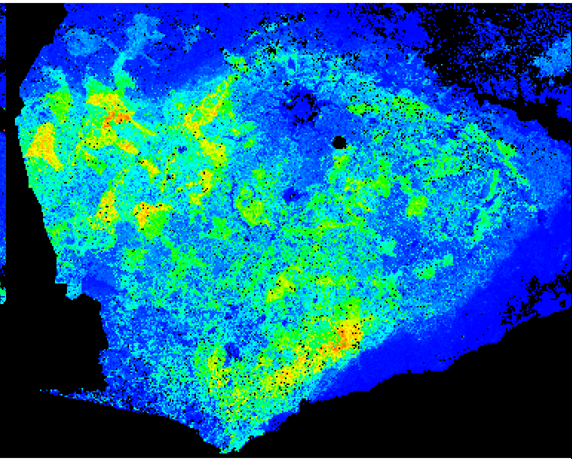


Scale of probabilities for Maxent predictions

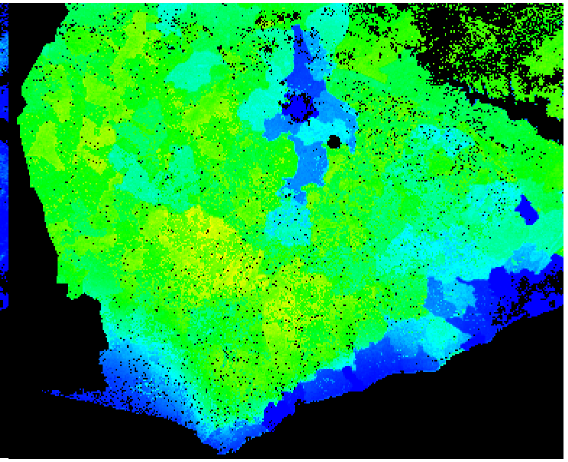
Figure 3.3: Distribution maps showing current probabilities of occurrence for large avian frugivores in the high forest zone of Ghana.



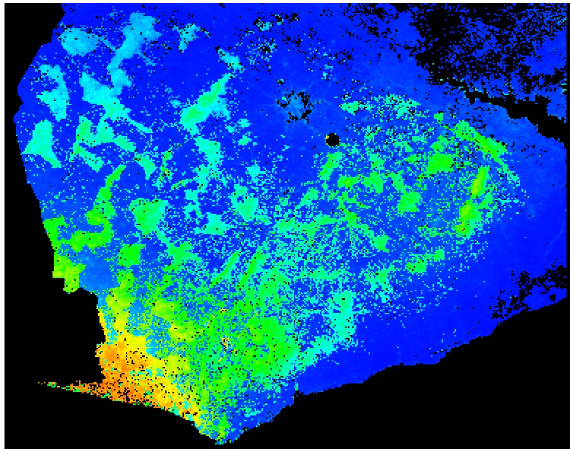
Grey Parrot



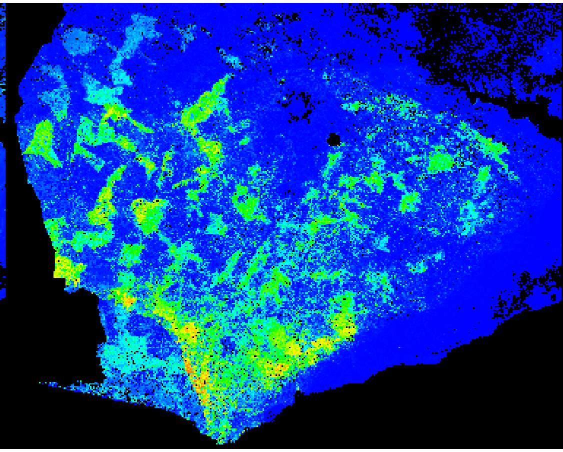
Red-fronted Parrot



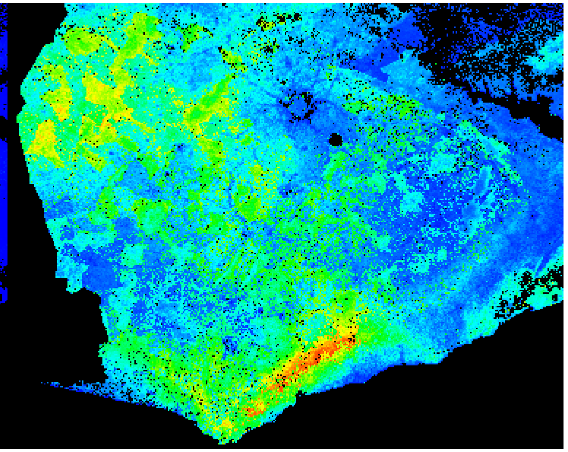
Brown-necked Parrot



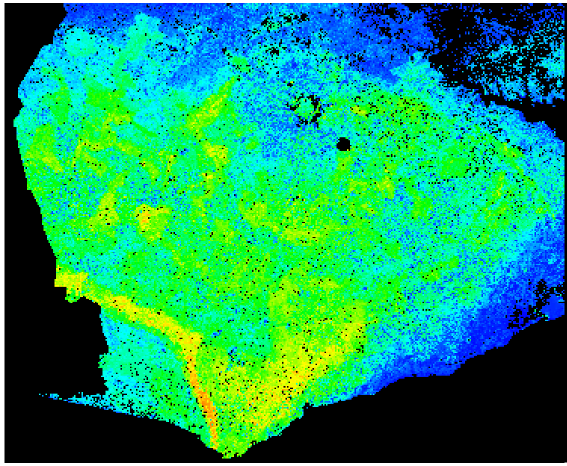
Great Blue Turaco

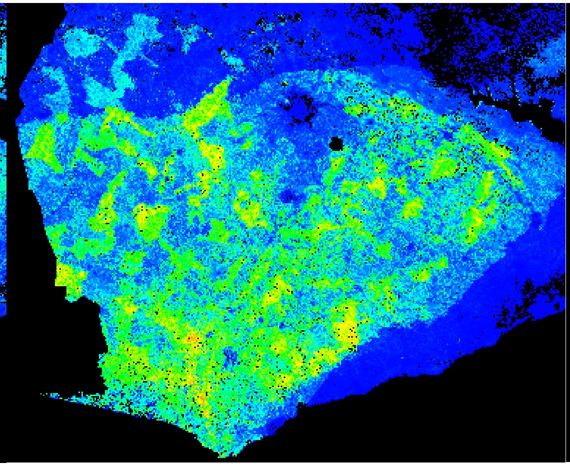


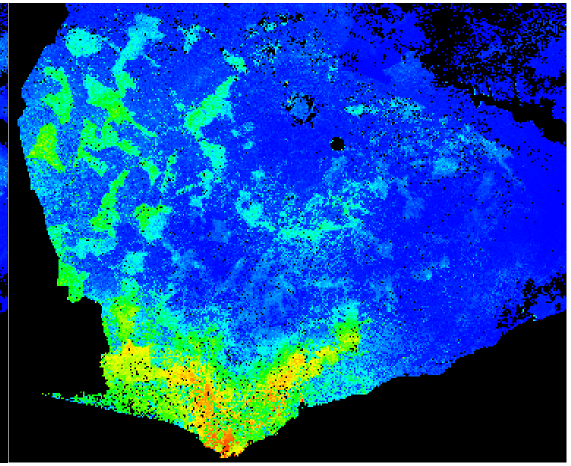
Yellow-billed Turaco



Green Turaco



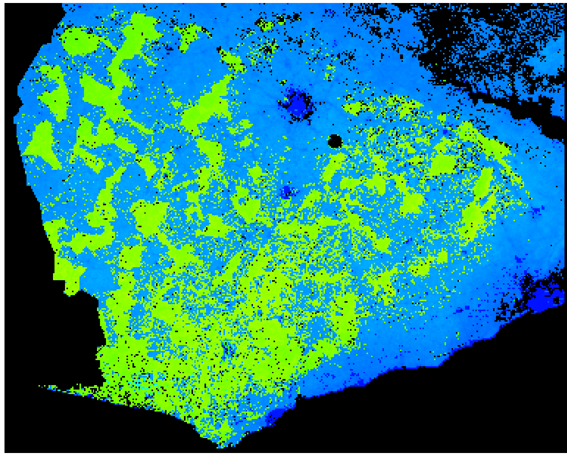


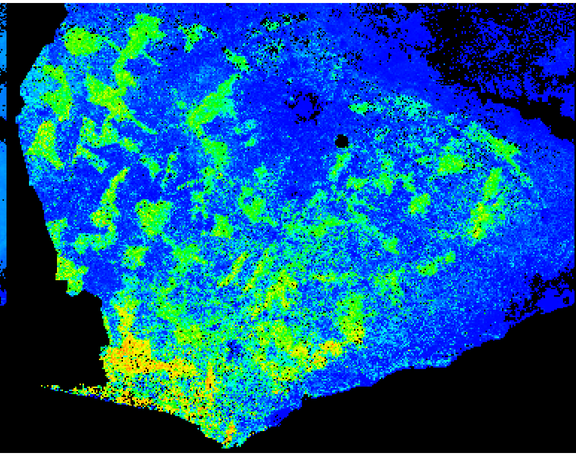


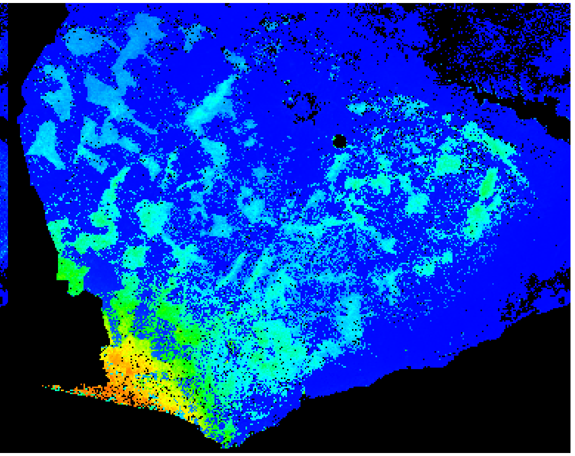
African Pied Hornbill

White-crested Hornbill

Piping Hornbill







Black Dwarf Hornbill

Red-billed Dwarf Hornbill

Yellow-casqued Hornbill

3.4.3 Environmental response curves

Land cover appeared in the top three variables in every one of the 15 species models (Figure 3.4). Annual rainfall was amongst the top three variables in 10 species models, seasonality of rainfall in eight, NPP in seven, both EVI and tree cover in three, and human population density in just one species model.

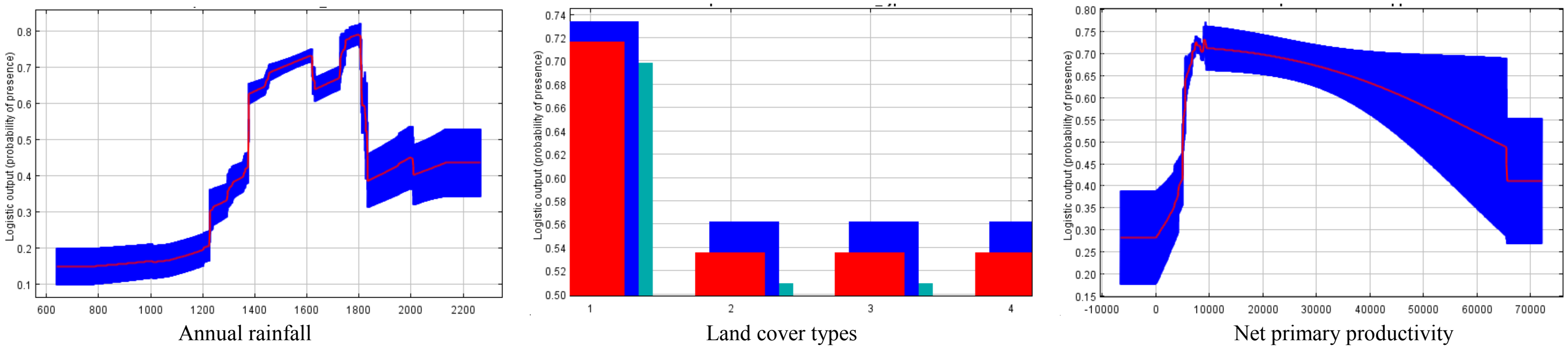
Land cover type was the most important predictor variable in the models for 12 species, with percentage contributions exceeding 40% in 11 species and greater than 90% in two species (Afep Pigeon and Black Dwarf Hornbill). Land cover type was the most important variable in six of the seven hornbills, all three turacos, along with both large pigeons (Afep and Western Bronze-naped). Of these 12 cases, forest was the preferred land cover type in every species except Green Turaco. Preference for forest over the other habitat types was strong in all these cases, especially the hornbills and large pigeons, which is also apparent from the probability of occurrence maps (Figure 3.3). In every species apart from Red-billed Dwarf Hornbill, either annual rainfall, seasonality of rainfall, or both, were among the top three predictor variables. However, these variables were only the top predictor in Green Pigeon and African Pied Hornbill (annual rainfall), and Brown-necked Parrot (seasonality of rainfall).

Several species have similar response curves for key variables. Brown-necked Parrot is unusual, in that land cover is of lesser importance, and it has a strong relationship with human population density – its probability of occurrence falls off sharply at anything but the lowest human densities (perhaps driven by high probability of occurrence in the north and northeast where human population is sparse). Only three species preferred any habitat other than forest. These were Grey Parrot (preferring both scrub and urban habitats), and Green Turaco and African Pied Hornbill (both preferring scrub over forest).

Table 3.4: Top three predictor environmental variables driving the distribution of large avian frugivores in Ghana. Figures in parentheses represent the percent contribution of each of the first three predictor variables to model construction.

Species	1	2	3
Grey Parrot	NPP (41.7)	Land cover (25.4)	Seasonality of rain (12.5)
Red-fronted Parrot	Land cover (35.9)	Annual rainfall (28.9)	EVI (15.7)
Brown-necked Parrot	Seasonality of rain (49.5)	Population density (26.0)	Land cover (15.1)
African Green Pigeon	Annual rainfall (34.1)	Land cover (28.3)	NPP (23.1)
Afep Pigeon	Land cover (91.9)	Seasonality of rain (6.5)	Percent tree cover (0.7)
Western Bronze-naped Pigeon	Land cover (67.7)	EVI (12.5)	Annual rainfall (6.3)
Great Blue Turaco	Land cover (68.4)	Annual rainfall (26.1)	EVI (5.2)
Yellow-billed Turaco	Land cover (52.9)	Annual rainfall (15.6)	NPP (13.1)
Green Turaco	Land cover (46.0)	Seasonality of rain (22.7)	Annual rainfall (11.2)
African Pied Hornbill	Annual rainfall (44.9)	NPP (31.4)	Land cover (12.4)
White-crested Hornbill	Land cover (47.9)	Annual rainfall (30.5)	Percent tree cover (7.6)
Piping Hornbill	Land cover (42.8)	Seasonality of rain (23.3)	NPP (14.9)
Black Dwarf Hornbill	Land cover (97.0)	NPP (1.0)	Seasonality of rain (1.0)
Red-billed Dwarf Hornbill	Land cover (65.3)	NPP (14.6)	Percent tree cover (12.7)
Yellow-casqued Hornbill	Land cover (59.1)	Annual rainfall (31.4)	Seasonality of rain (4.8)

African Green Pigeon: 34.1, 28.3, 23.1



Afep Pigeon: 91.9, 6.5, 0.7

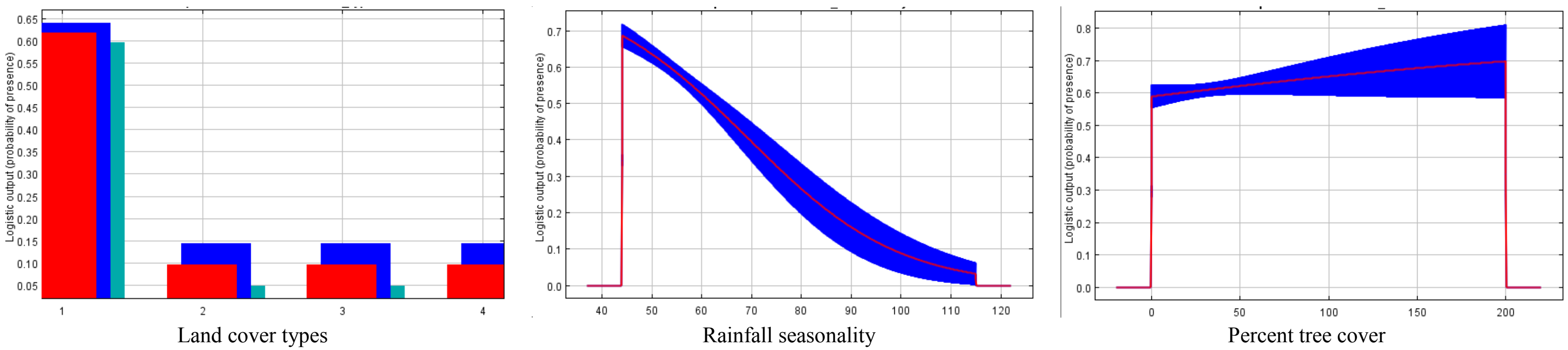
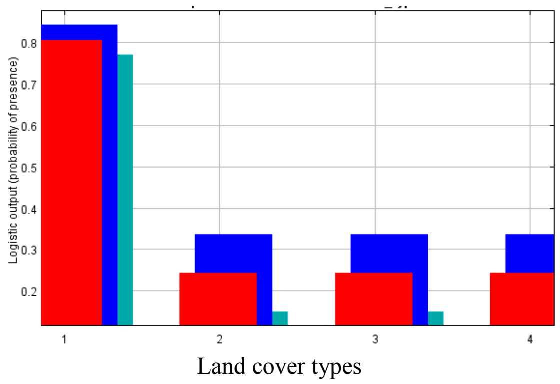
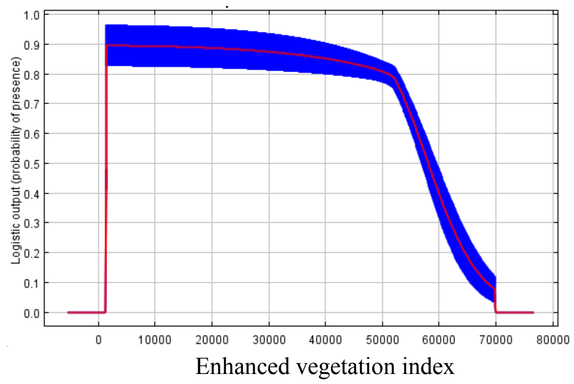


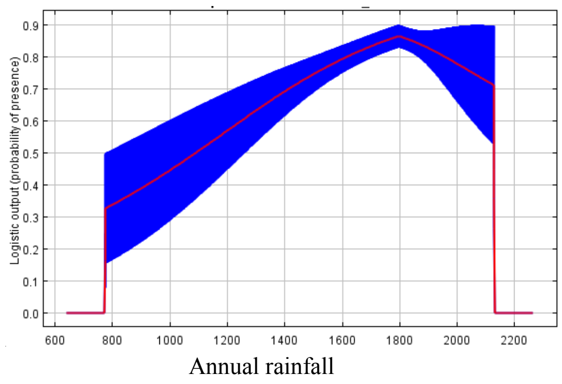
Figure 3.4: Graphs showing the influence of environmental variables on the probability of presence of the various species of frugivores during maxent model development. Figures following each species name refer to the percent contribution of the top three variables to models. Land cover types were classified into four categories where 1 = evergreen + decicuous forest, 2 = open + closed shrubland, 3 = cropland + natural vegetation and cropland, and 4 = urban + built-up areas.

Figure 3.4 Continued.

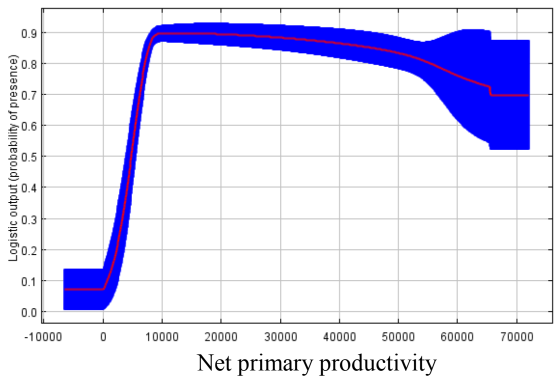
Western Bronze-naped Pigeon: 67.7, 12.5, 6.3

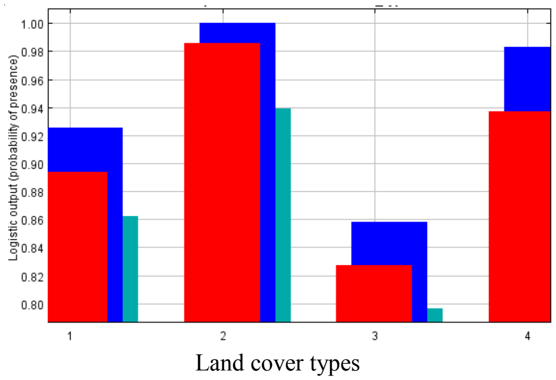






Grey Parrot: 41.7, 25.4, 12.5





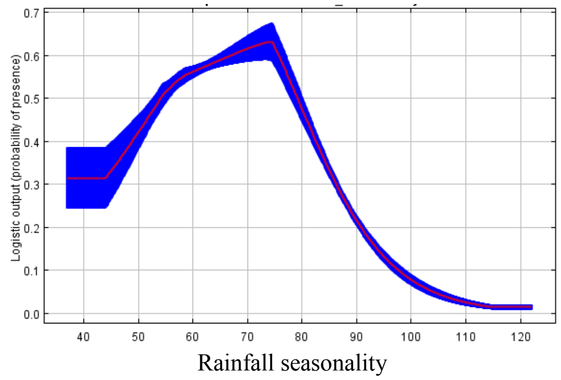
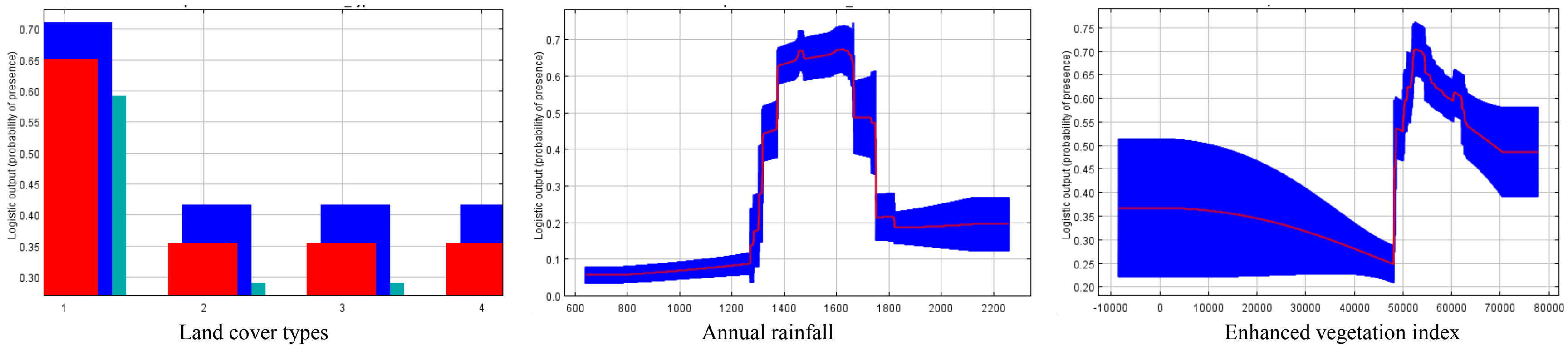


Figure 3.4 Continued.

Red-fronted Parrot: 35.9, 28.9, 15.7



Brown-necked Parrot: 49.5, 26.0, 15.1

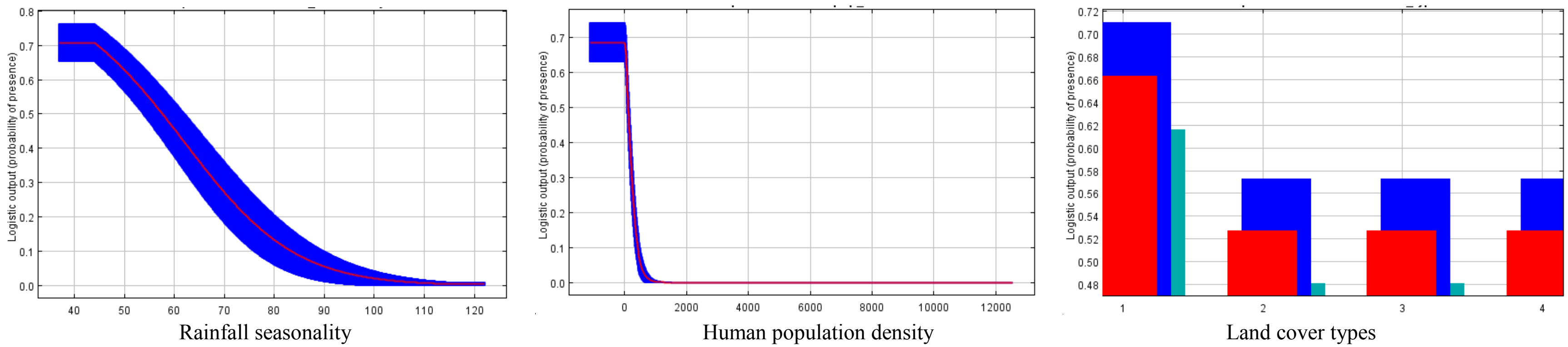
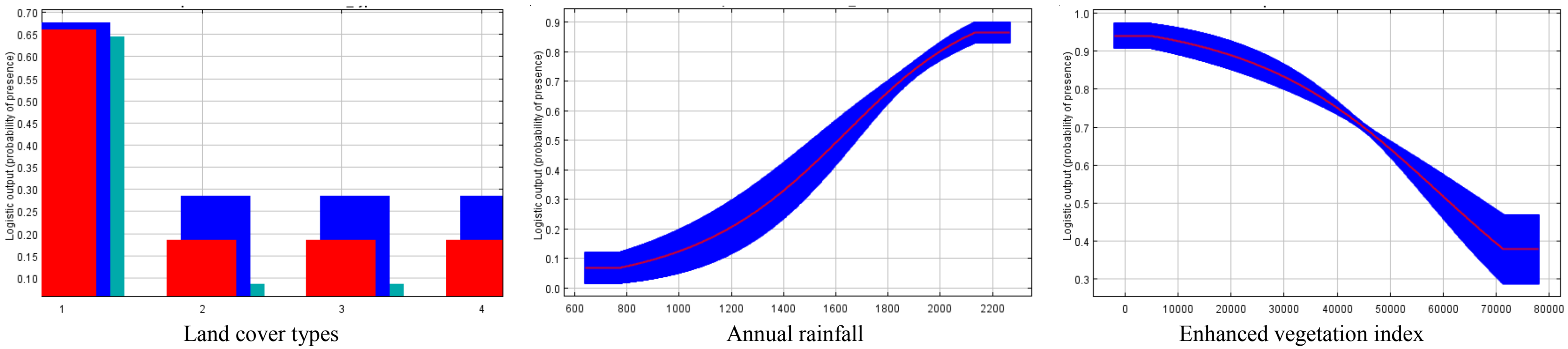


Figure 3.4 Continued.

Great Blue Turaco: 68.4, 26.1, 5.2



Yellow-billed Turaco: 52.9, 15.6, 13.1

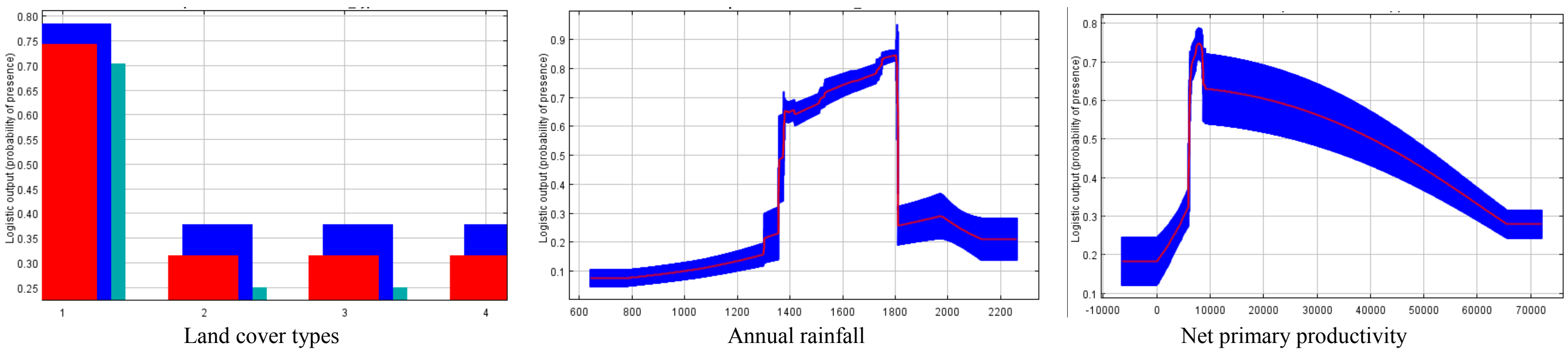
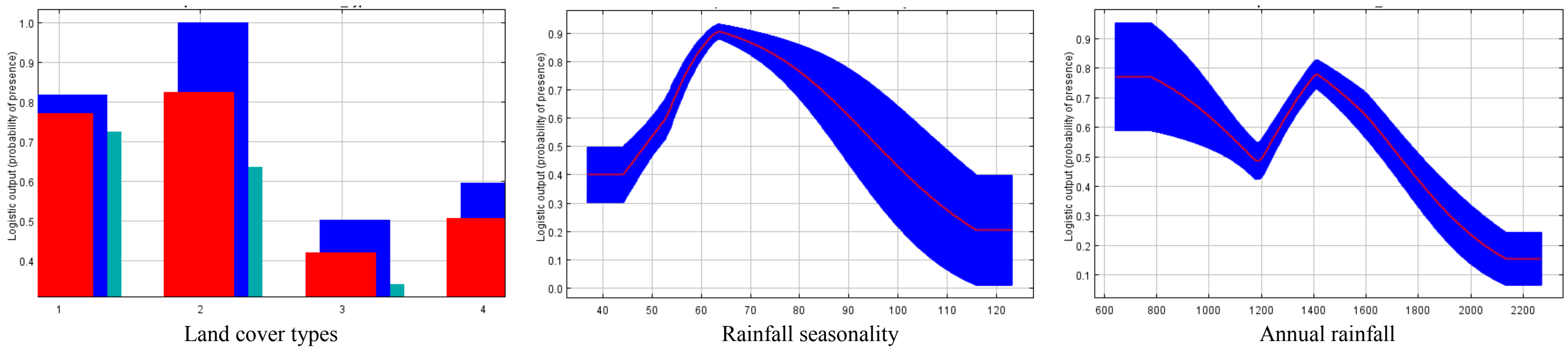


Figure 3.4 Continued.

Green Turaco: 46.0, 22.7, 11.2



African Pied Hornbill: 44.9, 31.4, 12.4

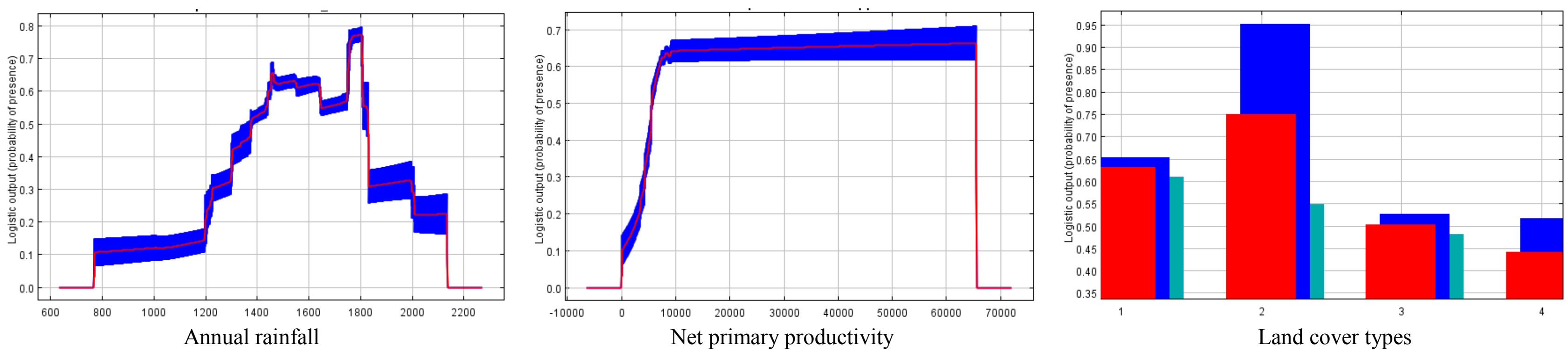
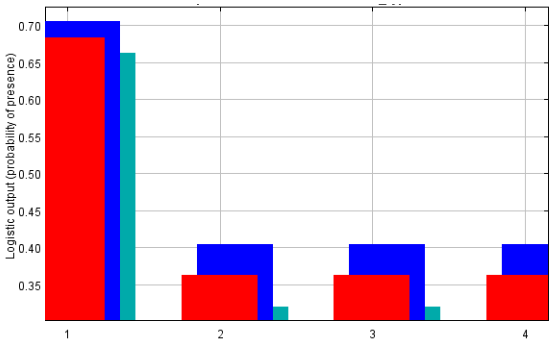
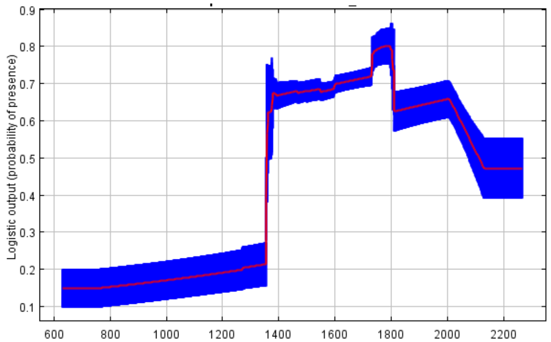


Figure 3.4 Continued.

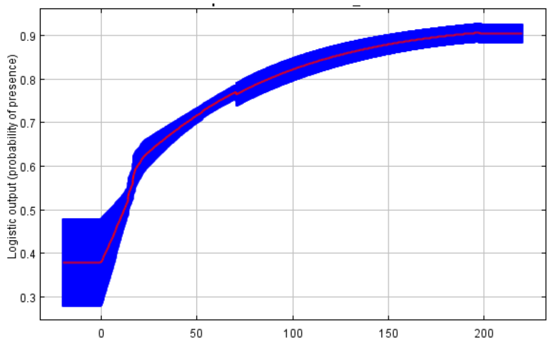
White-crested Hornbill: 47.9, 30.5, 7.6



Land cover types

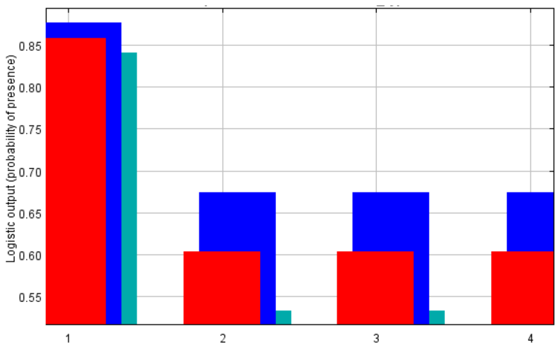


Annual rainfall

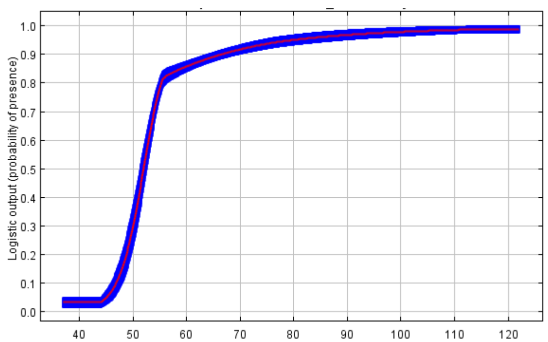


Percent tree cover

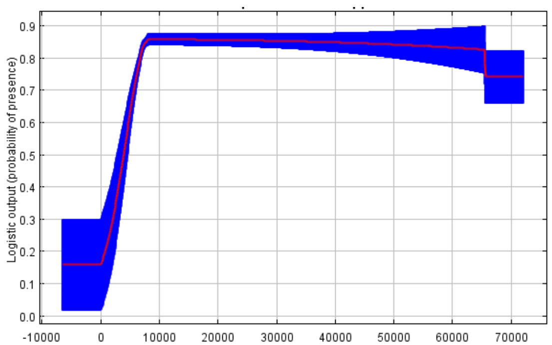
Piping Hornbill: 42.8, 23.3, 14.9



Land cover types



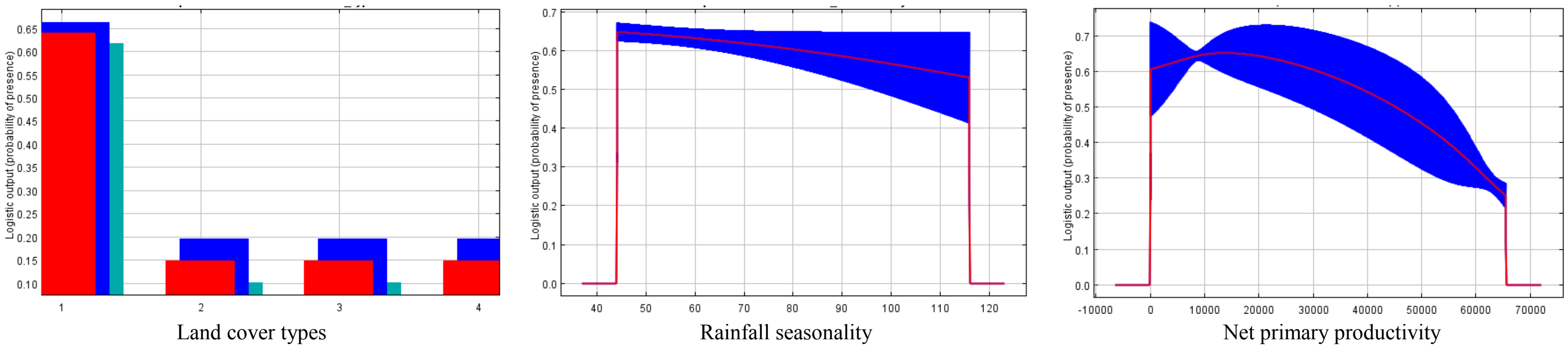
Rainfall seasonality



Net primary productivity

Figure 3.4 Continued.

Black Dwarf Hornbill: 97, 1, 1



Red-billed Dwarf Hornbill: 65.3, 14.6, 12.7

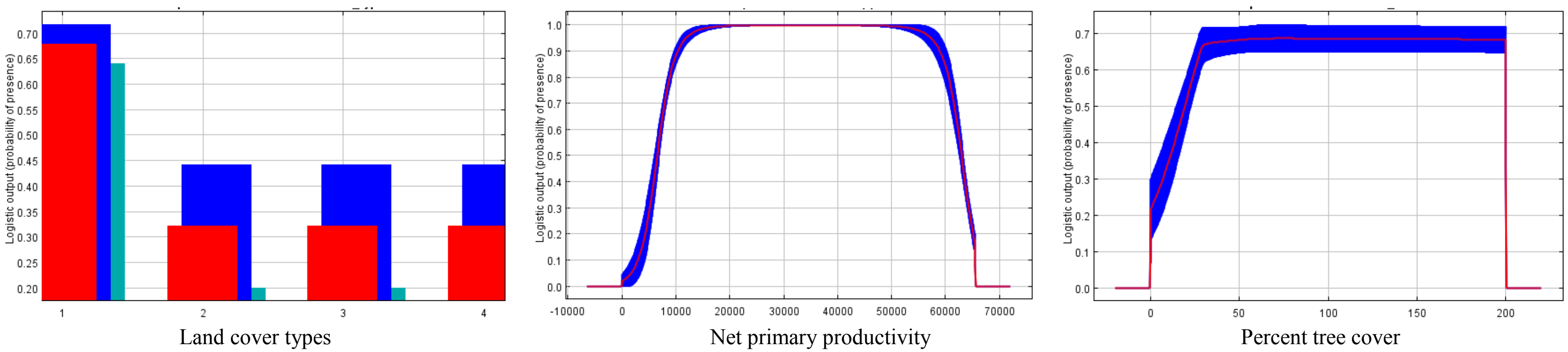
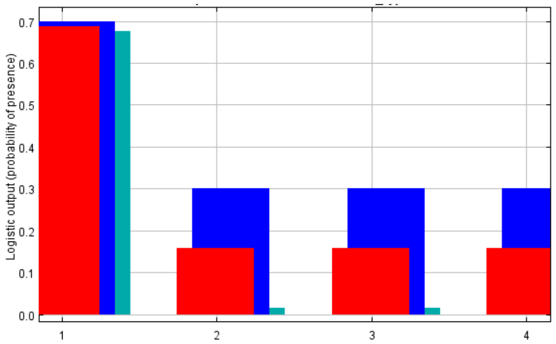
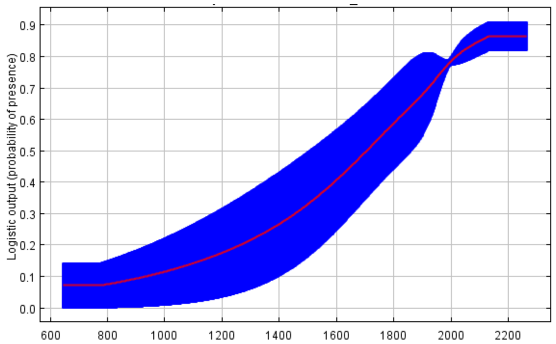


Figure 3.4 Continued.

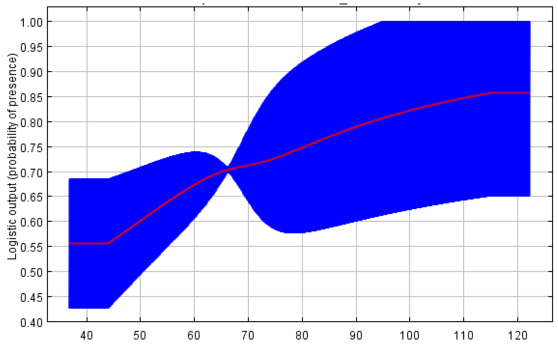
Yellow-casqued Hornbill: 59.1, 31.4, 4.8



Land cover types



Annual rainfall



Raifall seasonality

3.5 Discussion

Birds are considered to provide the most diverse range of ecological functions amongst vertebrate taxa (Sekercioglu 2006), and are mobile links essential for the maintenance of ecosystem function, memory and resilience (Lundberg and Moberg 2003). Avian frugivores, especially, are crucial for proper ecosystem function because of their role in maintaining forest structure (Cordeiro and Howe 2001, Sodhi et al. 2008). However, avian guilds such as frugivores and understorey insectivores suffer severe population declines following anthropogenic disturbance (Bregman et al. 2014). Large-bodied avian frugivore populations, especially, can be extirpated by forest loss, reduction in forest quality, and fragmentation (Bregman et al. 2014, Sreekar et al. 2015). It is therefore important to determine the distribution and abundance of key species across whole regions for biodiversity conservation purposes. SDMs such as Maxent enable us to predict the natural distributions of species for conservation decision-making, when well-designed survey data are analysed in conjunction with meaningful environmental predictors (Elith and Leathwick 2009, Guillera-Arroita et al. 2015). They have been used widely in various lines of scientific enquiry and Maxent, especially, has seen increased usage in the past decade. Examples of such studies range from predictions about the spatiotemporal distributions of endemic flora (e.g. Chitale et al. 2014), through the formulation of conservation targets for endemic lizards (e.g. Novaes e Silva et al. 2014) to predictions about current and future habitat availability for bird species (e.g. Monterrubio-Rico et al. 2015, Stiels et al. 2015). Few studies in West Africa have applied SDMs such as Maxent, and even fewer have directly involved Ghana (De Clercq et al. 2013, Läderach et al. 2013). Many avian studies that have applied Maxent SDM to frugivore populations have been monospecific or have examined a few species at a time (e.g. Cilliers et al. 2013, Trisurat et al. 2013, Jinamoy et al. 2014, Naniwadekar et al. 2015), and others have examined whole communities in regions or at landscape scales. However, a search of the scientific literature revealed that no study has employed Maxent SDM to examine the potential countrywide distribution of avian frugivores in Ghana. This study is therefore important, as it examines frugivore species distributions across the country's HFZ, an area that covers about a third of Ghana's landmass. Here, Maxent SDMs were used to map out the current distribution of avian frugivores over the entirety of Ghana's HFZ, and to determine which environmental variables might drive, or at least correlate with, observed patterns of distribution. All SDMs exhibited high levels of performance, and predicted very high PoOs for major species at key sites.

In this study, different species showed variable dependence on Ghana's large forest reserves. The SDMs indicate that more than a quarter of Ghana's large avian frugivores – African Green Pigeon, Brown-necked Parrot, Green Turaco and African Pied Hornbill – are widely distributed in the HFZ. The predicted distributions of these four species encompass the whole landscape. The members of this quartet are not forest obligates, as they occur over a variety of habitat types (Grimes 1987, Dowsett-Lemaire and Dowsett 2014) and potentially play a vital role in fruit and seed dispersal over the wider landscape. The African Green Pigeon, for example, is a forest and farmbush generalist and feeds on fig species (*Ficus spp*., Grimes 1987, Baptista et al. 2015) and many other fleshy-fruited species, a number of which are of direct economic importance (Dowsett-Lemaire and Dowsett 2014). African Green Pigeon and African Pied Hornbill have very similar predicted PoOs along similar areas in the southwest of the HFZ, especially along a narrow stretch of high PoO that appears to be the ecotone between the wet evergreen and moist semi-deciduous forest subtypes. For many species, namely Afep Pigeon, Western Bronze-naped Pigeon, Great Blue Turaco, Yellow-billed Turaco, Piping Hornbill, Black Dwarf Hornbill and Red-billed Dwarf Hornbill, their predicted distributions are restricted to forest reserves in the mid to northern margins of the HFZ. These species are less likely to be encountered in degraded intervening habitats such as farmland or fallows and suggests the unsuitability of such habitats for their persistence. Other species such as Western Bronze-naped Pigeon, Yellow-billed Turaco and Piping Hornbill are predicted to be restricted to forest reserves in the east and north of the HFZ but occur outside of forest reserves in the southwest. Piping Hornbill has a predicted distribution with very high PoOs in areas not far from the coast and around the forest reserves of Subri River, Cape Three Points, Draw River and Ankasa Wildlife Reserve. The species is shown to somewhat circumvent the centre of the HFZ, a phenomenon that remains unexplained (Dowsett-Lemaire and Dowsett 2014).

The key 'driver' of frugivore distribution was land cover (Table 3.4). This appeared important in all species. Forest was the most selected habitat type for the majority of species. Grey Parrot and African Pied Hornbill are predicted to prefer open or closed shrubland. This finding concurs with knowledge already available about the ecology of the two species. The Grey Parrot is often found in open shrubland provided such habitats supply resources such as fruiting trees for foraging or as roosts, or even nest-sites (Dändliker 1992, McGowan 2001, Clemons 2003). African Pied Hornbill has a ubiquitous distribution over the country, is found in all habitat types, and forages regularly in open shrubland (Dowsett-Lemaire and Dowsett 2014). Rainfall was of lesser importance generally, but in some species (e.g. African Green Pigeon and African Pied Hornbill), it was important in determining 'basal' distribution – with most species associated with the wetter parts of the country. The amount of rainfall and its seasonality as well as other climatic variables are often used in SDMs and found to be important (e.g. Abolafya et al. 2013, Duan et al. 2014). Other variables, especially human population density, were poor predictors of distribution.

3.6 Conservation and management implications

Ghana's forest reserves are crucial for the conservation of large frugivores, which in turn are crucial to forest conservation itself (Sekercioglu 2006, Whelan et al. 2015). There were sharp boundaries between high and low predicted occupancy for most species, especially large hornbills, turacos and Afep and Western Bronze-naped pigeons. The future of these species is undoubtedly linked to the persistence of forest reserves. Habitat connectivity is undoubtedly vital to the dispersal of forest dependent species in agro-managed landscapes (Rosenberg et al. 1997). However, Ghana's protected forests have become increasingly isolated 'islands' in a predominantly degraded matrix (Holbech 2009). This is particularly concerning since the suitability of the matrix has declined in the last three decades owing to increased felling of trees for lumber, agricultural intensification, and increased urbanisation (see Donkor and Vlosky 2003). Ghana's increasing human population size—which increased from 8.5 million in 1970 to 24.2 million in 2010, at rates well over 3% per annum (National Population Council of Ghana 2006, 2011)—is likely a major underlying factor that influences these adverse impacts. Despite the protection status of forest reserves and national parks, there is high hunting pressure on large avian frugivores (Dowsett-Lemaire and Dowsett 2014). The species of this guild are usually on the top of hunters' lists after large and small mammals are extirpated from forests (Holbech 1998, Waltert et al. 2010, Holbech 2014). It is important to note that Maxent predicts occupancy and not actual abundance of species (Phillips et al. 2006), so many of these frugivores could be quite rare in some reserves. All protected areas appeared to be important but the best reserves for large avian frugivores in Ghana are in the southwest of the HFZ, especially in the Ankasa area, Cape Three Points, and Subri River forest reserves. It is essential that these areas are given better protection through increased patrol effort, as this approach has previously proved effective in Ghana (Jachman 2008). Many large frugivores e.g. hornbills, have wide ranges, and tend to make nomadic movements over the seasons while tracking food resources (Kitamura 2011). It is therefore important to maintain connectivity between these reserves by ensuring rigorous protection for forest corridors that link substantial forests, as these species become prone to hunting when they cross wide-open habitats. Additionally, the establishment of diverse agro-ecosystems (*sensu* Holbech 2009) can contribute to a network of corridors that link the major forest reserves of southwest Ghana. Other frugivorous taxa such as primates need improved protection as they complement the role of avian frugivores (Albert et al. 2013).

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Chapter 4

TRADE AND HABITAT CHANGE VIRTUALLY ELIMINATE THE GREY PARROT *PSITTACUS ERITHACUS* FROM GHANA

4.1 Abstract

The heavily traded Grey Parrot *Psittacus erithacus* is believed to have undergone rapid population decline, yet there are almost no quantitative data on abundance changes over time from anywhere within its huge range. I reviewed the species' historical abundance across Ghana, undertook targeted searches during 3- to 5-day visits to 42 100-km^2 cells across the country's forest zone, repeated counts at 22 parrot roosts first performed two decades ago and gauged around 900 people's perceptions of the decline and its causes. In over 150 days of fieldwork, just 32 groups (maximum group size = 12) were recorded in 10 cells. Encounter rates averaged 0.15 individuals per hour of targeted search, around 15 times lower than those recorded in the early 1990s. No active roosts, i.e. roosts in current use, were found, and only 18 individuals were recorded in three roost areas that each harboured 700–1200 birds two decades ago. Interviewees stressed the importance of very tall trees of commercially important species such as *Terminalia superba* and *Ceiba pentandra* for nesting and roosting, and believed that the felling of large trees on farmland (42% of responses) and trapping for trade (37%) were the two main causes of decline. Ghana has lost 90–99% of its Grey Parrots since 1992, a time when the population had presumably already been seriously reduced by two decades of extremely heavy trade. There is no evidence that, away from one or two localities, declines are less severe anywhere else within the West African range of *P. erithacus*, or across the entire range of the recently split Timneh Parrot *Psittacus timneh*.

4.2 Introduction

Efforts to assess long-term changes of global populations of birds are often hampered by a lack of quantitative data on historical abundance. Baseline historical data against which contemporary repeat surveys can be directly compared are powerful tools in quantifying the extent and degree of declines (Prakash et al. 2003, Alderman et al. 2011) but the existence of such data is rare. More usually, concern for the status of a species triggers dedicated surveys, which have to be compared with anecdotal information about historical abundance (e.g. Cuthbert et al. 2009). An exacerbating issue with very wide-ranging species is that abundance and population trajectories may be uneven across their extent of occurrence, making it difficult to characterize declines accurately and assign causes (Senyatso et al. 2013).

The Grey Parrot *Psittacus erithacus* (until recently considered conspecifc with the Timneh Parrot *Psittacus timneh*) is widely distributed, with a range of nearly 3 million km^2 from Côte d'Ivoire and Ghana in West Africa, through Nigeria and Cameroon and the Congo forests, to Uganda and western Kenya (del Hoyo and Collar 2014). Over recent decades, it has been among the most traded of all birds listed under CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora). CITES-reported imports of Grey Parrots from all range countries totalled 847,525 between 1980 and 2014 (http://trade.cites.org/). However, owing to unreported domestic trade, mortality between capture and sale, and considerable unreported international trade, a more realistic figure for the numbers taken from the wild between 1982 and 2001 alone could have exceeded one million (BirdLife International 2015).

The impact of this trade on wild populations is easy to imagine but difficult to quantify. A recent review lists multiple reports of severe declines across much of its range, but these are based on anecdotal evidence and/or questionable or non-comparable methods (Martin et al. 2014). Added to this, recent extensive surveys of Grey Parrot, using distance sampling (e.g. Buckland et al. 2008), found highly variable local abundances—very low densities at sites in Liberia, Cote d'Ivoire and Democratic Republic of the Congo (DRC), but remarkably healthy densities in parts of Cameroon and on the island of Príncipe in the Gulf of Guinea (Marsden et al. 2015). An accurate rate of overall decline has, therefore, proved elusive but, given the enormous levels of offtake for the trade acting concurrently with habitat loss, a decline of 30–49% in three generations (47 years) is currently assumed, qualifying the species as 'Vulnerable' according to IUCN Red List criteria (BirdLife International 2015).

An unpublished but technically meticulous CITES study which reported Grey Parrot encounter rates and examined parrot abundance at 22 roosts in the early 1990s (Dändliker 1992) provided a unique opportunity to (longitudinally) gauge the degree of decline experienced in Ghana over the past 20–25 years. Using this baseline, the objectives of our study were fourfold. First, I compared the current distribution and abundance of the species across Ghana with historical data from various sources. Second, I repeated the series of 1990s roost surveys undertaken by Dändliker to quantify the decline in the species. Third, I used structured interviews to gauge knowledge and perceptions of the decline in Grey Parrots and its possible causes. Fourth, I examined historical and current trade and other factors likely to have contributed to the decline in the species.

4.3 Methods

4.3.1 Historical and current status of the Grey Parrot in Ghana

I first reviewed information on the species' historical status from published and unpublished reports of previous surveys, involving some of the earliest scientific information on the species from last century, through surveys conducted in the 1970s, to the most recent work on the species in the 1990s. These included encounter rates for the species calculated by Dändliker (1992), both from his surveys, and from those from studies between 1976 and 1978 conducted by the Ghana Wildlife Division (GWD) in and around the village of Achiase (Aykease) in the Central Region. Dändliker himself surveyed parrots from 'fairly randomly chosen' points across his study area during around 30 mornings and evenings. He counted mostly flying parrots which included both movements of birds to roosts and flights of 'local breeding birds'. His surveys were conducted during 24 days in Western and Central regions, 5 days in the Volta region, 10 days in the Northern region, and 6 days in Ashanti and Brong-Ahafo regions).

To assess current distribution and abundance, 50,000 km^2 of 75,000 km^2 of the historical range of the species within Ghana (areas in the west and southwest that were most likely still to hold the species) were partitioned into a grid of 100 km^2 cells. A sample of 42 cells was selected, not randomly, but to maximise the likelihood of encountering Grey Parrot populations (Figure 4.1). This, itself, was based on historical records of the species and the presence of substantial forest cover. Each cell was visited for periods of 3–5 days, between April 2012 and June 2014, with parrot surveys conducted on each day between 05h45 and 11h00. Surveys were conducted by walking along hunter or farmer footpaths and along drivable pathways connecting villages and/or towns. Survey routes traversed a variety of habitats including small-scale agroecosystems, large-scale oil palm plantations, forest reserves and settlements. I walked survey routes in the company of a local guide, and all individual Grey Parrots heard or seen along the route, perched or in flight, were recorded together with direction of flight and GPS coordinates at the point of detection. Furthermore, long watches were conducted from vantage points between 16h00 and 18h00 on some days, timed to correspond with the periods of afternoon flight towards roosts (Wirminghaus et al. 2001, Amuno et al. 2007).

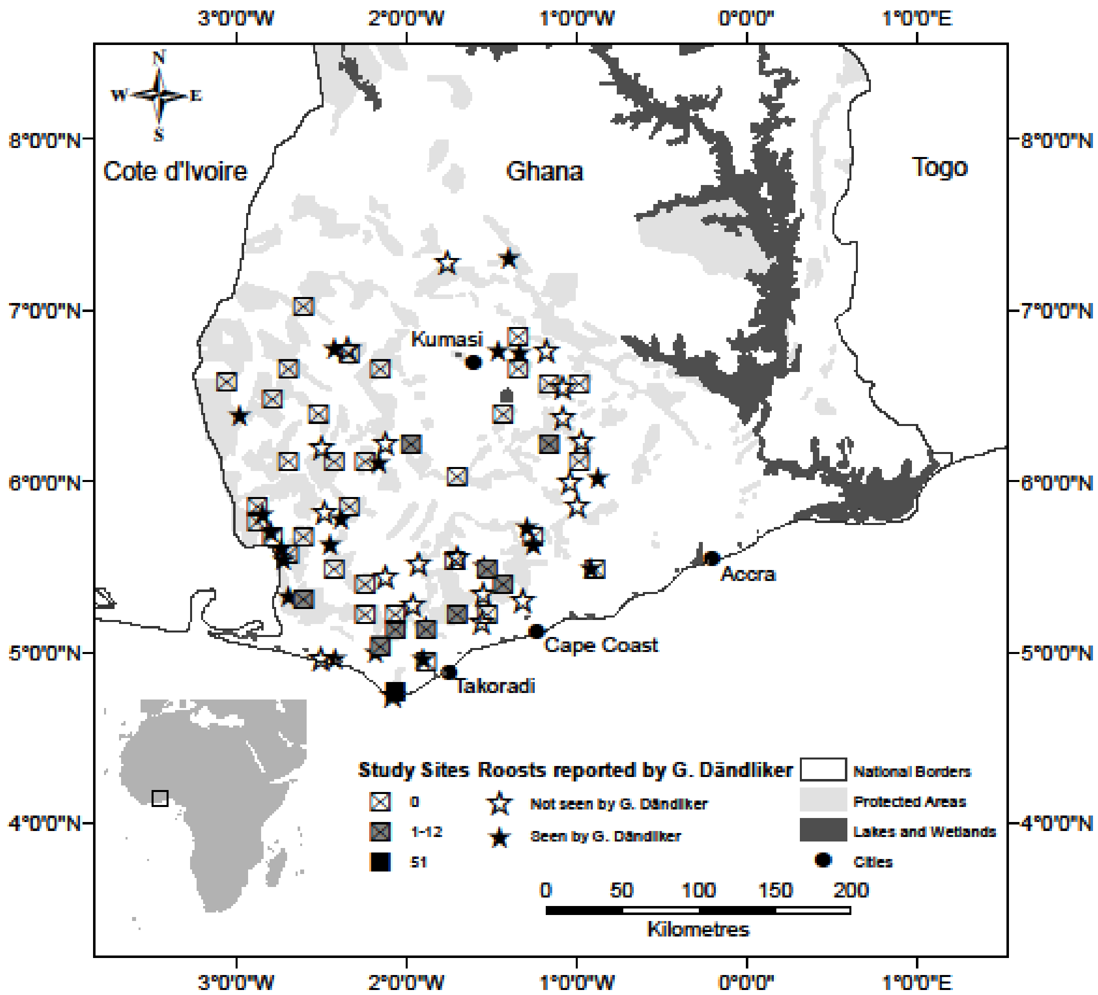

Figure 4.1: Map of southern Ghana showing positions of 42 sampled cells, parrot records, roost sites visited, and protected areas. Note that surveys and roost searches were focused on the historical range of the species in the southwest of the country.

4.3.2 Roost counts in 1991–2 and 2014

Dändliker (1992) travelled around Ghana in December 1991 and January 1992 identifying 60 roosts/roost areas using the local knowledge of parrot trappers and officials from the Ghana Wildlife Division (see Appendix 1 for locations). He and his assistants visited 22 roost areas, and actually counted parrots (on either one evening or an evening and one morning) at 15 of these. I visited 42 of the 60 roost areas, and all 22 actually visited by Dändliker, between 2012 and 2014. Roost areas were sought, based on Dändliker's descriptions of location, for periods of 1–2 days. Former trappers or other knowledgeable local people would guide me to the known roost/former roost site and/or potential alternative roost/aggregation areas. If local people did not know any remaining roosts, bird surveys were conducted for two consecutive days, with special focus on potentially suitable habitats for parrot roosts, including swampy habitats (known often to be favoured by *Psittacus*: Forshaw and Cooper 1989).

4.3.3 Public perception and knowledge of Grey Parrots

Structured interviews were conducted in all the study cells and roost areas surveyed to obtain information about local people's knowledge of Grey Parrots and to investigate aspects of the parrot trade. The mean number of interviewees per cell was 17 ± 10 SD (range 3–45). On arrival at a village in a study cell, the chief or village leader and his/her elders were informed about the project. A field assistant subsequently walked around the village and interviewed any residents willing to respond to a set of questions from a prepared questionnaire.

A total of 906 people were interviewed within squares and during roost searches, although not all interviewees answered every question. Interviewees were asked when they had last observed Grey Parrots, whether they thought the species had declined, and the species of trees in which they knew Grey Parrots to nest, roost and feed, the height of trees used (> 30 m = 'Very tall'; 20–30 m = 'Tall'; < 20 m = 'Not tall'). Questions and possible responses are given in Appendix 2. The vast majority (97%) were male, 87% were aged 30 years or more and 52% were over 40 years old. Most (92%) had lived in their communities for over 10 years, and 85% were farmers. Just 0.2% were 'professional' hunters, although 1% stated hunting as a secondary occupation.

4.3.4 Historical and current trade in Ghanaian Grey Parrots

I explored the history of Grey Parrot trade in Ghana using relevant literature (Ussher 1874, Lowe 1937, Grimes 1987, Dändliker 1992, Dowsett-Lemaire and Dowsett 2014), and by interrogating the CITES trade database (accessed on 16/11/14 with search for reported live exports of the species from Ghana). I conducted detailed interviews with 29 bird traders in eight major urban centres in southern Ghana: Kumasi Central Market in Ashanti Region; Kantamanto, Malata and Madina Markets in Greater Accra Region; Assin Fosu, Twifo Praso and Kotokoraba Cape-Coast Markets in Central Region; and Takoradi Market Circle in Western Region (see Appendix 3 for GPS coordinates). Grey Parrots on sale in these markets or in villages during field visits were counted and vendors interviewed. Interviews were held with active, or previously active, Grey Parrot trappers throughout the study area.

4.4 Results

4.4.1 Historical and current status of the Grey Parrot in Ghana

Historically, the Grey Parrot occupied much of the forest zone of Ghana, occurring over approximately 75,000 km^2 of forest including the whole of the Western and Central Regions of the country, nearly the whole of Ashanti Region as well as the semideciduous forest areas of southern Brong-Ahafo Region, the western part of the Eastern Region, and parts of the Greater Accra Region (Bannerman 1931, Bouet 1961). The species is also reported to have been present in riparian forests of the savanna zone of the Northern Region, but there are no data indicating that it was present in seemingly suitable habitat in the Volta Region of (easternmost) Ghana (Dändliker 1992). Despite the sense in the 1940s that the species might have been declining in some areas owing to trade, large flocks of 500–1,000 parrots could then still be observed (Grimes 1987). Four decades later (1988), large flocks of 2,000–3,000 continued to occur in parts of the parrot's range in Ghana (Dändliker 1992). Data from studies between 1976 and 1978 conducted by GWD in and around the village of Achiase (Aykease) in the Central Region, and analysed by Dändliker (1992), produced an average Grey Parrot encounter rate of 1.5–1.9 birds per hour (mean of 52 counts). Fifteen years after the GWD studies, Dändliker (1992) recorded Grey Parrot encounter rates of 1.1–1.3 birds per hour near the Achiase area. From 30 morning/evening counts across his whole study area, encounter rates averaged 1.9–2.4 per hour.

By 1992, around 60 Grey Parrot roosts (although perhaps not all active at one time) had been identified within Ghana. Individual roosting areas in Ghana appear to be used over several years (Dändliker 1992), as they are elsewhere (e.g. Cameroon: Fotso 1998), although the precise location of the roost within the area might shift. It might also be expected that numbers of Grey Parrots using roosts might change seasonally or even daily, as in other parrots (Amuno et al. 2007). Roosts were distributed throughout the forest zone, with the distance of any given roost to the three nearest roosts averaging 27 km; altogether 130–210 roosts were thought to exist within the forest zone (Dändliker 1992). Roost density was estimated at 0.18–0.27 per 100 km^2 and, allowing for varying abundances in different forest types, the national population was extrapolated as 30,000–80,000 Grey Parrots (Dändliker 1992). In a multi-species forest bird study between June 1995 and August 1996, Grey Parrots were found in 'more than 20' of the 28 forest reserves studied, but only 87 groups were recorded during the entire survey period (Ntiamoa-Baidu et al. 2000).

In my surveys, a total of 32 groups, comprising 103 individual Grey Parrots, were recorded in ten (24%) of the 42 squares surveyed (Figure 4.1). Only one of these groups was actually recorded perched. The amount of time spent surveying in each square ranged between 12 and 21 hours of actual field effort. Mean encounter rate across all sites was 0.047 ± 0.14 (SD) groups per hour (0.15 ± 0.51 individuals per hour). Half of all birds encountered (51 of 103) were recorded in one square, and exclusion of this square reduces mean encounter rates to 0.026 ± 0.059 (groups) and 0.077 ± 0.18 (individuals). Mean group size was 3.2 (modal group size, occurring 13 times = 2; max. group size = 12).

4.4.2 Roost counts in 1992 and 2014

Of the 60 roosts and roost areas identified by Dändliker (1992), I visited 42 (70%; Appendix 1). Not a single active roost was found, although Grey Parrots were seen within a few kilometres of five former roosts. The largest number of birds (51) recorded during four days of surveys within a single square was counted in and around the village of Douahohorodo, a roost identified by Dändliker (1992) but one which he failed to locate in his surveys. Only 11 and 7 Grey Parrots, respectively, were counted near two of Dändliker's (1992) three biggest roosts of 700–1,200 birds each. No parrots were found at the third roost area, where the vegetation is currently dominated by unshaded cocoa *Theobroma cacao* plantations. A proper assessment of changes in vegetation at roosts between 1992 and 2014 was impossible, but Dändliker's original descriptions of habitat type tended to match fairly well with that found in 2014 (Appendix 1). Habitat changes are, however, likely to have occurred, including increased prevalence of oil palm, drainage of and planting on raffia swamp, and the cutting of individual large trees which were the focus of some roosts in 1992 (Appendix 1).

4.4.3 Public perception and knowledge of Grey Parrots

Of 866 respondents, 27% stated that they had last observed Grey Parrots within the previous year, 41% 1–5 years previously, 22% 6–10 years previously and 9% over 10 years previously. In only five (12%) of the 42 squares surveyed was there no report of a parrot sighting in the previous year. However, 94% of 846 respondents believed there to have been a decline in Grey Parrot abundance in the last five years, and 99% over the past 10–20 years. All 26 bird traders interviewed in major market centres in the south of Ghana thought there had been a major population decline in Grey Parrots, and that the current supply of birds was negligible.

Respondents stated that the most important tree species for nesting and roosting are *Terminalia superba* and *Ceiba pentandra*, with *Elaeis guineensis* most important for feeding (Table 4.1). A strong preference for very tall trees for nesting (93% of respondents) and roosting (95%) was reported, but none for tree heights for feeding. Of 889 respondents, 70% said nest trees were located outside rather than inside forest reserves. While I acknowledge potential upward bias in recording rates outside over those inside the forest, this at least indicates that parrots in Ghana do nest outside of reserves, as they do elsewhere (Twanza and Pomeroy 2011, Irumba 2013). Respondents attributed the decline in Grey Parrots to trapping for trade, felling of large trees on farms, or both (Table 4.2). Hunting for food was very seldom cited as a reason for declines, as was mechanised logging alone, although the latter was deemed more important when coupled with loss of farm trees.

Table 4.1: Main tree species used by Grey Parrots for nesting, roosting and feeding. The relative importance of each species is indicated by the number/percentage of times it was mentioned by the 906 respondents.

Species	Nesting	Roosting	Feeding
Terminalia superba **(Ofram)**	433 (34.6%)	468 (36.5%)	37 (3.0%)
Ceiba pentandra **(Onyina)**	236 (18.9%)	232 (18.1%)	46 (3.7%)
Milicia (Chloroplora) excelsa **(Odum)**	221 (17.7%)	204 (15.9%)	113 (9.1%)
Celtis mildbraedii (C. zenkeri) **(Essah)**	61 (4.8%)	57 (4.5%)	172 (13.8%)
Elaeis guineensis **(Oil palm)**	3 (0.2%)	58 (4.5%)	497 (40.0%)
Raphia **spp. (Raffia)**	2 (0.2%)	41 (3.2%)	185 (14.9%)
Other species (Other)	295 (23.6%)	222 (17.3%)	193 (15.5%)
Tree heights			
Very tall (> 30 m)	743 (92.8%)	732 (95.2%)	216 (26.4%)
Tall (20-30 m)	45 (5.6%)	22 (2.9%)	291 (35.6%)
Not tall (< 20 m)	13 (1.6%)	15 (2.0%)	311 (8.0%)

4.4.4 Historical and current trade in Ghanaian Grey Parrots

Large numbers of Grey Parrots were already in trade in Accra and Cape Coast in the 1870s (Ussher 1874, Dowsett-Lemaire and Dowsett 2014). In his account of expeditions to the Gold Coast in the 1930s, Lowe (1937) expressed hopes for the recovery of Grey Parrot populations in the country owing to the closure of the live bird trade in England, indicative of potentially appreciable exports to the latter country. The 'large numbers' of parrots traded historically from Ghana remain, however, unquantified (Ussher 1874, Lowe 1937). A trade with neighbouring countries in Grey Parrot body parts may have begun in the mid-1970s (Dändliker 1992). In the early 1970s, Ghanaian Muslims on the Hajj pilgrimage to Mecca began exporting Grey Parrots to Saudi Arabia for resale (Dändliker 1992). This novel and lucrative trade went largely unscrutinised by Ghanaian officialdom and involved large numbers of parrots: at its peak up to 20,000 birds annually were being moved without documentation by air, both as cargo and as hand luggage. Trade via this route flourished until Saudi Arabia placed an embargo on parrot imports in 1986 (Dändliker 1992). Meanwhile, several thousand Grey Parrots were also being exported annually through Ghana's neighbouring countries such as Côte d'Ivoire, Togo, Mali and Benin, as far as Senegal, for re-export to Europe and USA (Dändliker 1992).

Table 4.2: Responses of interviewees concerning the main factors they considered to be drivers of declines in Ghana's Grey Parrots. Responses are split according to whether the factor was identified as acting alone or with other factors. Figures are shown for combinations of factors ('with other factors') only if numbers are greater than 20. Figures in parenthesis are the percentage of times a particular response was given either alone or along with other factors.

Factor	**Alone**	**With other factors**	**Total**
Hunting for food (H)	7 (1.7)		29 (2.3)
Trapping for trade (T)	211 (49.8)	172(+F); 30(+L); 41(+FL)	463 (36.8)
Felling farm trees (F)	178 (42.0)	172(+T); 127(+L); 41(+TL)	533 (42.3)
Mechanised logging (L)	28 (6.6)	127(+F); 30(+T)	234 (18.6)

Commercial trade in Grey Parrots underwent several periods of embargo in Ghana after 1967 until, in May 1980, a ban on exports was imposed owing to suspicions that the species was being used to smuggle diamonds (Dändliker 1992). Bans and revocations were repeated multiple times between 1980 and 1989, until the last ban, still in force owing to lack of data for establishing an export quota, was effected in 1994 (CITES 2012). CITES-reported exports from Ghana averaged 3,047 ± 3,234 (SD) per annum between 1976 and 1990. Reported export numbers were highly variable in these fifteen years, ranging from 0 in 1976 to 9,585 in 1978 and 8,680 in 1985 ((http://trade.cites.org/). CITES-reported exports averaged just 2 per annum in the years 1991–2012.

During my fieldwork five recently caught Grey Parrots were found for sale in three markets—two in separate stalls at Kantamanto, two at Kumasi, and one at Assin-Fosu. The traders concerned stated that these five individuals had been bought from trappers in the previous few months. All 26 dealers who gave an opinion reported that the trade collapsed many years previously, and that current supply is based on opportunistic trapping by villagers. These dealers kept large stocks of parrots in their market aviaries in the mid- to late 1990s, and had an abundant supply from trappers. According to seven dealers, current (2014) prices were variable (mean = 700 ± 621 SD Ghana Cedis; approx. US$230) but two dealers stated that Grey Parrots could sell for 1,000–2,000 Ghana Cedis (approx. US$330–660) if bought by expatriates. These prices contrast strongly with those from the early 1990s when birds were bought from trappers for US$8–12, and passed on from dealer to exporter usually for less than US$20 (Dändliker 1992).

No currently operating parrot trappers could be found to interview. Of 23 former trappers interviewed, 17 had become farmers and only one admitted having trapped a

Grey Parrot in the previous year. Two others had trapped Grey Parrots in the previous five years but 15 stated that they had not caught any in the previous decade. Nine trappers stated that their livelihoods from Grey Parrot trapping became unsustainable in the mid-1990s when parrot populations declined, and many of their fellow-trappers emigrated to other countries including Côte d'Ivoire, Liberia and even DRC to ply their trade. Besides Grey Parrots, interviewees indicated that during the 1980s they trapped other species including Red-headed Lovebird *Agapornis pullarius*, Red-fronted Parrot *Poicephalus gulielmi*, West African Pied Hornbill *Lophoceros semifasciatus*, Western Long-tailed Hornbill *Horizocerus albocristatus*, Yellow- and Black-casqued Hornbills *Ceratogymna elata* and *C. atrata*, African Green-pigeon *Treron calvus*, and Great Blue Turaco *Corythaeola cristata* (taxonomy follows del Hoyo and Collar 2014).

4.5 Discussion

Grey Parrot populations in Ghana have declined catastrophically over the past 20 years. I posit that this decline is certainly in excess of 90%, and could be as high as 99%, as evidenced by the near-total loss of the major roosts known in 1992 (Dändliker 1992). This said, Grey Parrots were recorded in one quarter of surveyed squares, and small numbers do remain over quite large areas of the country—a pattern shown elsewhere in Africa of significant numerical contraction with little or no distributional change (e.g. Kori Bustard Ardeotis kori: Senyatso et al. 2013). Results of this study largely concur with a recently published Ghana bird atlas (Dowsett and Dowsett-Lemaire 2014) which found, at a coarse scale, that Grey Parrots were still present in very small numbers across much of the southwest of the country; periods of 3–5 day visits to eight forest reserves in 2008–9 yielded sightings of single pairs (three reserves), single birds (three reserves) and no birds (two reserves).

Encounter rates of 0.15 individuals per hour (around one group per 2–3 days) of targeted searching over wide areas indicate the enormity of the decline since previous studies, which recorded encounter rates of around 2 individuals per hour in the 1990s (Dändliker 1992). While comparisons of encounter rates presented in different studies are problematic, these findings are further reinforced by interviewees' perceptions and a general lack of observations.

4.5.1 Causes of decline

I identify four factors that can confidently be regarded as having contributed to the decline of the Grey Parrot in Ghana: trade, overall forest reduction, silvicultural practice, and farmland timber harvesting.

The CITES trade database has Grey Parrot imports originating from Ghana totalling 67,259 birds for the period 1976–1990 (www.unep-wcmc-apps.org/citestrade). Allowing for domestic consumption, which does not appear in CITES trade figures, high pre-export mortality (variable, but averaging around 50% from capture to market: Clemmons 2003), and the absence of data on presumably significant illegal trade in official reports (Pain et al. 2006), the real number taken from the wild in Ghana in this period is probably far higher and plausibly well over twice as many. Dändliker (1992) estimated annual offtake levels in excess of 10,000, and up to 20,000 birds during years of maximum trade, between the early 1970s and late 1980s. The heavy trade in the 1970s and 1980s presumably contributed significantly to population declines well before Dändliker's surveys. However, most striking is the fact that, in the years 1991–2012, when trade was outlawed and Ghana's CITES-reported exports of Grey Parrots totalled just 35 individuals (2 per annum), the population in the country still declined by 95%. Given that interviewed trappers still held large numbers of Grey Parrots in the mid-1990s, this illegal trade must surely have contributed to the post-1990 declines that I report; however, since some trappers judged the trade unsustainable from the mid-1990s the bulk of the illegal trade may have occurred in the years immediately after 1992. It is also possible that heavy capture of juveniles in the decades preceding 1992 had left the Grey Parrot population with a highly skewed age structure. Parrots are long-lived (Forshaw and Cooper 1989), and a significant time lag might have fallen between the perturbation and the resultant decline of the species (Marsden and Pilgrim 2003, Hylander and Ehrlen 2013).

Logging and farming are major causes of forest loss and alteration in Ghana, compounded by poor forest management, fire and mining (Benhin and Barbier 2004). Ghana's human population increased from 8.5 million in 1970 to 24.2 million in 2010, at rates well over 3% per annum (National Population Council of Ghana 2006, 2011, Ghana Statistical Service 2012). This rapid population growth has shortened fallow periods and increased demand for land (Donkor and Vlosky 2003). At the time of Dändliker's survey in 1992, forest cover totalled 74,480 km^2, whereas by 2010 it had fallen by a third to 49,400 km^2 (http://rainforests.mongabay.com/deforestation/2000/Ghana.htm). This clearly represents a significant reduction of Ghana's carrying capacity for Grey Parrots.

Reduction in habitat quality, especially in terms of the removal of large trees, is another important factor in parrot declines (e.g. Manning et al. 2013). Parrots typically nest in very large trees (e.g. Marsden and Jones 1997, Monterrubio-Rico and Enkerlin-Hoeflich 2003), and Grey Parrots are no exception (Clemmons 2003, Valle *et al*. in prep.). In the 1970s and 1980s, the practice of 'salvage logging' was probably particularly detrimental to Ghana's Grey Parrots, as this permitted the unlimited felling of large trees as a means of 'cleansing' forests of over-mature timber, regarded as undesirable under national forest management policy (Hawthorne and Abu-Juam 1995, Dykstra et al. 1996, Benhin and Barbier 2004).

Licensed logging of individual trees in agricultural areas evidently further damaged Grey Parrot populations, particularly given that 70% of interviewees reported the species nesting outside of forest. Over 50% of timber harvests in Ghana during the period 1972–1992 were from outside reserves, with farmers having no legal rights to timber trees on their land and receiving little or no compensation from loggers for crop damage during felling (Sargent et al. 1994). Crucially, this circumstance remains a disincentive to retain trees on farmland and contributes heavily to the pre-emptive destruction of large trees outside forest reserves (Ruf 2011).

4.5.2 The status of Grey and Timneh Parrots across West Africa

More than six months of dedicated searching within likely areas of Ghana, including visits to roosts which previously held 700–1,200 individuals, yielded just a handful of Grey Parrot sightings. Undoubtedly, the species has declined precipitously, and is now extremely rare across Ghana. Is there any evidence that the Grey Parrot and its recently split sister species Timneh Parrot are anything but similarly rare in any other part of West Africa (west of Cameroon)? The answer, I suspect, is no: both species have been virtually eliminated from wider landscapes, and exist in reasonable numbers at very few locations.

Such sites include the Bijagós Islands, Guinea-Bissau (Martin et al. 2014), and perhaps parts of the Gola Forest in Liberia and Sierra Leone, where flocks of around 70 Timneh Parrots have recently been recorded (Author pers. data, C. Showers in litt. 2013). Interestingly, Liberia appears to have retained its larger animals relatively well (Tweh et al. 2015), and further work might find small parrot populations elsewhere in the country. However, densities elsewhere within the Timneh's range appear extremely low (Martin et al. 2014): for example, around 32 km of distance sampling line transects and 38 hours of dedicated encounter rate survey within Parc National d'Azagny and other likely areas in Cote d'Ivoire yielded not a single record of the species (Marsden et al. 2015). The situation for Grey Parrot in West Africa is quite possibly worse, with the species being probably extinct in Togo, and very rare right across Nigeria (McGowan 2001, Green et al. 2007, Martin et al. 2014).

Absence of evidence that any *Psittacus* populations in the region are healthy must surely now preclude trade from West Africa, and calls into question considerations of further trade in much of mainland Central Africa. Both Grey Parrot and especially the much smaller-ranged Timneh Parrot are surely now candidates for reconsideration of their Red List categorisation.

4.6 References

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4.7 Appendices

Appendix 4.1: Counts of Grey Parrots at roosts identified by Dändliker (1992) in Ghana's high forest zone, and repeat counts from the current study. Figures in parentheses refer to estimated roost sizes by Dändliker (1992). Scientific names of species are given only on first mention. GD = G. Dändliker, NA = N. Annorbah, GP = Grey Parrot.

	Dändliker (1992)			**This study**			**Notes**
	Roost location	**Habitat**	**Count#**	**Location revisited**	**Habitat**	**Count**	
1	Abroadziwuram 1°33'58"W 5°09'30"N	Not seen (riverine raffia palm *Raphia* spp.)	Not seen	Yes	Raffia palm, riparian forest	Nil	NA: former trappers blamed population collapse on both trapping and removal of big trees on farmland
2	Mpohor 1°54'39"W 4°58'8"N	Oil palm *Elaeis guineensis* plantation	100–200	Yes	Oil palm	Nil	GD: Disturbance from hunters, including gunshots. NA: No GPs seen in either plantations or neighbouring habitats.

	Dändliker (1992)			This study			Notes
	Roost location	**Habitat**	**Count#**	**Location revisited**	**Habitat**	**Count**	
3	BOPP (Benso Oil palm Plantation) 1°52'52"W 5°09'09"N	Oil palm plantation	800–1,200	Yes	Oil palm plantation	11	GD: Disturbance from hunters, including gunshots. NA: Flocks of 2 and 5 birds flew over plantation and 4 in farmland nearby but residents say roost is not present anymore.
4	Kambungli 2°25'18"W 4°59'12"N	Riverine raffia swamp	Nil	Yes	Riverine raffia and mangrove *Avicennia germinans* and *Rhizophora* spp. swamp	Nil	GD: Raffia palms reportedly utilised seasonally during May–July when fruits sprout. NA: Widespread raffia and mangrove habitats.

	Dändliker (1992)			This study			Notes
	Roost location	**Habitat**	**Count#**	**Location revisited**	**Habitat**	**Count**	
5	Amansuri 2°30'39"W 4°58'30"N	Not seen (raffia palms along river)	Not seen	Yes	Raffia and mangrove swamps along river	Nil	NA: Surveyed areas along the Amansuri river and around north of Beku, as described by GD.
6	Dominase 2°11'24"W 5°00'59"N	Riverine raffia palm and bamboo *Bambusa* spp.	15	Yes	Riverine raffia palm and bamboo	2	GD: GPs seen in neighbouring villages. NA: GPs seen in riparian forest along Ankobra River.
7	Appiakrom 2°27'5"W 5°37'33"N	Raffia palm swamp	50 (> 200)	Yes	Raffia, secondary growth and cocoa	Nil	GD: Exact location not determined. Roost said to have moved some distance away prior to survey. NA:

	Dändliker (1992)			This study			Notes
	Roost location	Habitat	Count#	Location revisited	Habitat	Count	
					Theobroma cacao		Raffia swamps in area but cocoa forms majority of habitat.
8	Nsabrekwa 2°23'10"W 5°48'11"N	Raffia palm swamp	70 (200–250)	Yes	Raffia, oil palm, cocoa, secondary growth	Nil	GD: Roost probably disturbed by trappers. GD's guide allegedly saw about 500 GPs days earlier. NA: Raffia swamps abound but cocoa forms majority of habitat.
9	Peinikrom 2°50'58"W 5°49'15"N	Small oil palm plantation	30	Yes	Oil palm and cocoa	Nil	GD: Birds settled in palms. Roost disturbed prior to assessment. NA: Many old emergent oil palms popular with GPs present but cocoa forms major habitat.

	Dändliker (1992)			This study			Notes
	Roost location	**Habitat**	**Count#**	**Location revisited**	**Habitat**	**Count**	
10	Amonie 2°48'07"W 5°42'52"N	Raffia palm swamp	700–1,000	Yes	Raffia swamps but mostly cocoa	Nil	GD: GPs located in extensive raffia swamp 1.5 km from village. NA: Many swamps replaced by cocoa plantations; small-scale mining widespread in area.
11	Omanpe 2°44'12"W 5°37'11"N	Oil palm plantation and raffia swamp	8	Yes	Oil palm, raffia and cocoa	Nil	GD: Parrots flew towards plantation but not the raffia swamp. NA: Cocoa forms major habitat.
12	Boinso 2°43'08"W 5°33'17"N	Raffia palm swamp	4–6, 20 flew over	Yes	Cocoa, riverine forest, and scattered raffia swamps	Nil	GD: Reports of disturbance from trappers over previous night. About 400 GPs reportedly counted by GD's guide previous day. NA: Cocoa forms major habitat.

	Dändliker (1992)			This study			Notes
	Roost location	**Habitat**	**Count#**	**Location revisited**	**Habitat**	**Count**	
13	Boin-Tano 2°41'42"W 5°19'48"N	Raffia swamp	30–40 flew over	No	Raffia swamps but mostly cocoa in surrounding areas	Nil	GD: Roost not found but parrots flew over to another location. NA: Failed to reach the confluence of the two rivers but surveyed surrounding areas.
14	Ahweafutu 2°59'10"W 6°23'60"N	Raffia palm swamp	Nil	Yes	Mostly cocoa, with few emergent trees	3	GD: Roost attacked with guns few days prior to visit. NA: Birds flew over but no roost located. Habitat is a 'sea' of cocoa with emergent trees.
15	Bonwire 1°27'54"W 6°45'57"N	Raffia palm swamp	Nil	Yes	Farmland, remnants of raffia palms,	Nil	GD: Believed roost not in use for a couple of years. NA: Large oil palm plantation nearby.

	Dändliker (1992)			This study			Notes
	Roost location	Habitat	Count#	Location revisited	Habitat	Count	
					bamboo, old tall oil palm		
16	Maudaso 2°9'59"W 6°7'20"N	Raffia palm swamp	40	Yes	Mostly cocoa, oil palm, bamboo, secondary growth	Nil	GD: Unsure if location was indeed a roost as may have been a tree on which parrots settle prior to flight to roost. NA: Very widespread surface-mining has destroyed much raffia habitat.
17	Ntom/Bethlehem 2°7'50"W 6°13'43"N	Not seen	Not seen	Yes	Oil palm, cocoa		NA: GPs said to have been common in the past.
18	TOPP (Twifo Oil palm Plantation)	Oil palm plantation	1,000–1,200	Yes	Oil palm plantation	7	GD: GPs heavily disturbed by trappers and shooters on the plantation. NA:

	Dändliker (1992)			This study			Notes
	Roost location	**Habitat**	**Count#**	**Location revisited**	**Habitat**	**Count**	
	1°32'54"W 5°30'48"N						Large portions of plantation replaced with new palm.
19	Foso-North 1°17'55W 5°44'38"N	Oil palm plantation	350	Yes	Old oil palm plantation	Nil	GD: recent roost, probably offshoot from recently disturbed one at Kwatta (No. 17). NA: Roost no longer present but seasonal visits by a few pairs of GP reported by farm owner.
20	Kwatta 1°15'26"W 5°38'37"N	Oil palm plantation	Nil	Yes	Oil palm, coconut palm *Cocos nucifera*, small-scale agriculture	Nil	GD: Roost abandoned owing to pruning and harvesting of the palm, or an attack by trappers. NA: Exceptionally high numbers (hundreds at a time) of African Pied Hornbills seen.

	Dändliker (1992)			This study			Notes
	Roost location	Habitat	Count#	Location revisited	Habitat	Count	
21	Tarkwa Banso 1°57'51"W 5°17'19"N	Not seen (raffia swamp)	Not seen	Yes	Raffia swamp	Nil	NA: Extensive swamps in the area, but large-scale industrial mining as well.
22	Hemang Prestea 2°7'50"W 5°26'11"N	Not seen (raffia palms)	Not seen	Yes	Raffia and bamboo	Nil	NA: Not much left of the raphia palms along the sides of the Pra river near the town.
23	Kusi 0°52'58"W 6°02'01"N	Oil palm plantation	50–100	Yes	Oil palm plantation	Nil	GD: 30 more GPs flying to another roost. NA: Plantation workers say roost no longer present and GPs not seen in past few years.
24	Kuranti 1°55'43"W 5°32'13"N	Not seen (oil palm plantation)	Not seen	Yes	Oil palm, raffia swamps	Nil	NA: Many raffia swamps in area, plus oil palm plantations

	Dändliker (1992)			This study			Notes
	Roost location	**Habitat**	**Count#**	**Location revisited**	**Habitat**	**Count**	
25	Dadiesoaba 2°25'40"W 6°47'22"N	*Ceiba pentandra* tree	Nil	Yes	Oil palm, raffia palm and secondary growth forest	Nil	GD: Roost claimed by locals to have moved to the nearby Disiri Forest Reserve. NA: Cocoa forms major habitat. Surveys of Disiri FR did not yield any GPs.
26	Disiri 2°21'2"W 6°46'40"N	Forest Reserve	Not seen	Yes	Forest with extensive teak (*Tectona grandis*) plantation.	Nil	NA: Forest heavily degraded through illegal logging, many parts clear-felled for farmland.
27	Ntunkumso 1°20'4"W 6°45'36"N	Oil palm plantation	60–100	Yes	Oil palm plantation	Nil	GD: Alleged shooting of GPs by hunters shortly before his counts. NA:

Dändliker (1992)				This study			Notes
	Roost location	Habitat	Count#	Location revisited	Habitat	Count	
							Oil palm still present but mostly replanted.
28	Wiawso 2°30'39"W 6°11'35"N	Not seen	Not seen	Yes	Peri-urban with surrounding farmland and old growth fallow	Nil	NA: Surveyed area surrounding originally described location by GD.
29	Juaso area 1°04'44"W 6°33'12"N	Not seen (oil palm plantation)	Not seen	Yes	Cocoa, oil palm, secondary growth	Nil	GD: Old information and reported to be in a big oil palm plantation. NA: Landscape dominated by cocoa and oil palm.

	Dändliker (1992)			This study			Notes
	Roost location	Habitat	Count#	Location revisited	Habitat	Count	
30	Akutuase 1°10'48"W 6°46'18"N	Not seen (raffia swamp)	Not seen	Yes	Farmland, secondary growth	Nil	GD: NA: Report of a former large roost on a cliff surface in the area. GPs said to have disappeared since.
31	Ofinso (Nsanua) 1°45'23"W 7°16'44"N	Not seen	Not seen	Yes	Grassland, farmland, riparian forest	Nil	GD: Reported to be 20 km north of Kumasi, near Ofinso. NA: Imprecise location by GD. Actually located 70 km north of Kumasi in transition type riparian forest typified by surrounding *Borassus* palm and grassland.
32	Ochiso 0°55'28"W 5°30'06"N	*Ceiba pentandra* tree	100	Yes	Oil palm, coconut palm, secondary growth	Nil	GD: Roost allegedly held 600 GPs two years earlier. NA: Much oil palm felled for wine tapping.

	Dändliker (1992)			This study			Notes
	Roost location	**Habitat**	**Count#**	**Location revisited**	**Habitat**	**Count**	
33	Ntronang 1°05'05"W 6°22'34"N	Not seen (Oil palm plantation)	Not seen	Yes	Oil palm, cocoa	Nil	NA: Surveyed oil palm plantations and along the Pra River in the vicinity of Ntronang (now a big town).
34	Abenase 1°2'36"W 6°0'15"N	Not seen (oil palm plantation)	Not seen	Yes	Oil palm plantations	Nil	GD: Roost said to be an oil palm plantation near village. NA: surveyed area in different habitats including oil palm.
35	Asuansi 1°19'21"W 5°18'02"N	Not seen (oil palm)	Not seen	Yes	Oil palm, *Citrus* sp. and secondary growth forest	Nil	NA: Surveyed areas surrounding the village, especially Oil palm plantations.

	Dändliker (1992)			This study			Notes
	Roost location	**Habitat**	**Count#**	**Location revisited**	**Habitat**	**Count**	
36	Wassa Atobiase 1°33'15"W 5°20'31"N	Not seen (oil palm)	Not seen	Yes	Cocoa, oil palm	Nil	NA: Raffia and bamboo swamps present
37	Atieku 1°42'10"W 5°33'59"N	Not seen (Oil palm plantation)	Not seen	Yes	Oil palm, old growth fallow, raffia swamps	Nil	NA: Potentially suitable habitat, next to a forest reserve.
38	Odumasi (Asankraguaa) 2°29'35"W 5°49'15"N	Not seen (*Ceiba pentandra* tree)	Not seen	Yes	Cocoa and riparian forest	Nil	NA: Flock of 12 Red-fronted Parrots *Poicephalus gulielmi* seen in area. Shown a tree in a cocoa farm where GPs used to feed.
39	Kwae 0°58'40"W 6°14'04"N	Not seen (oil palm)	Not seen	Yes	Oil palm plantation,	Nil	NA: Huge oil palm plantation for the Ghana Oil palm Plantation Development Company (GOPDC)

	Dändliker (1992)			This study			Notes
	Roost location	Habitat	Count#	Location revisited	Habitat	Count	
					secondary growth forest		
40	Douahohorodo (Dixcove) 2°4'59"W 4°45'21"N	Raffia palm swamp	Not seen	Yes	Mangrove/raffia swamp, oil palm	51	GD: Not found. NA: Spent three days searching. GP flock sizes ranged from 1 to 12; bird flight paths suggested movement between the mangrove and the Cape-3-Points Forest Reserve.
41	Achiase 1°0'27"W 5°51'44"N	Not seen (raffia palm swamp)	Not seen	Yes	Oil palm, bamboo swamps, farmland	Nil	NA: Interviewed two former trappers who worked on the 1976–1978 GWD studies and assisted Dändliker (1992) during his survey.

	Dändliker (1992)			This study			Notes
	Roost location	**Habitat**	**Count#**	**Location revisited**	**Habitat**	**Count**	
42	Abrimaso 1°23'59"W 7°19'13"N	Forest reserve	32+	Yes	Transition type forest	Nil	GD: Counted GPs in area but did not actually see a roost. NA: Brown-necked Parrot *P. robustus* and Senegal Parrots *P. senegalus* abundant in reserve.

Appendix 4.2: Structured questionnaire showing list of questions and possible answers administered during surveys in the study area. Note questionnaire also includes open-ended questions.

Date:	Latitude:
Place:	Longitude:
Interviewer Name:	Others Present:

PART I: PERSONAL DETAILS

1. Gender: Male □ Female □
2. Age: <30yrs □ 30-40yrs □ 41-50yrs □ >50yrs □
3. Number of dependants: 0-3 □ 4-6 □ 7-9 □ ≥10 □
4. Educational background: Primary □ Secondary/Vocational □ Tertiary □
5. Religion: Christianity □ Islam □ Traditionalist □ Other……………...
6. In which town/village do you live? …………………………………………………
7. Length of stay: Visitor □ 1-3yrs □ 4-6yrs □ 7-9yrs □ ≥10yrs □
8. Occupation: Primary………………..… Secondary…………………………

PART II: KNOWLEDGE ABOUT GP

9. When did you last see GPs?..
10. Where did you see them?...
11. How many GPs did you see?...
12. What were the GPs doing? e. g. perched, flying, feeding, etc…………………
13. What tree species do GPs
    a) Feed on?………………………………………………………………
    b) Roost on?..……………………………………………………………
    c) Nest on?..
14. How tall are the trees mentioned in Q13 a, b and c?
    a) i) Not tall ii) Tall iii) Very tall
    b) i) Not tall ii) Tall iii) Very tall
    c) i) Not tall ii) Tall iii) Very tall

Not tall: < 20 m; Tall: 20-30 m; Very tall: > 30 m.

15. At what height on trees is a nest usually located?..

a) Not high on trunk b) High on trunk c) Very high on trunk d) In crown of tree

Not high: below mid-section of trunk; High: above mid-section of trunk; Very high: just below crown of tree.

16. Where are these trees (Q13-15) located?...

a) Forest Reserves b) Outside of Forest Reserves

17. What is your impression of current GP abundance compared to:

a) 1 yr ago: i) increased ii) not changed iii) decreased

b) 5 yrs ago: i) increased ii) not changed iii) decreased

c) 10 yrs ago: i) increased ii) not changed iii) decreased

d) 20 yrs ago: i) increased ii) not changed iii) decreased

18. Which of the following factors do you think account(s) for the trend in Q17 above?

a) Hunting b) Trapping c) Felling of trees on farmland d) Mechanized logging

19. Do you know of any GP roost, past or present?..

20. If yes to Q19, how many birds are/were there in this roost?..............................

21. Do you know of any GP nest?..

22. If yes to Q21, can you locate this GP nest?..

PART III: SOCIO-ECONOMICS OF GP

23. Is it easy to come by GPs for the trade these days compared to the past?............

24. Do you know how to trap GPs in the wild?..

25. When was the last time you trapped GP?...

26. How many GPs have you trapped since the beginning of this year?..................

27. How many GPs did you trap last year?...

28. How many trapped GPs die out of every 10 caught birds?.................................

29. Of every 10 trapped GPs, how many are

a) Juvenile?.... b) Immature?..... c) Adult?…..

30. Where do you sell trapped GPs?

a) Local buyer b) Retailers come to buy c) Transported to big city

31. How much is a bird sold to the following buyers?

a) Local buyer b) Retailers who come to buy c) Buyers in the big city

32. Does the price of GP vary during the year? a) Yes b) No

33. If yes to Q32, does it increase or decrease and what time/season of year?……

34. Are you able to meet the demand for GPs throughout the year? a) Yes b) No

35. What is the price of a GP at the following times?

a) Now:…………. b) 10 years ago:………….. b) 20 years ago:…

36. What other species of parrot and frugivorous birds do you trap or hunt?.............

37. Are these other species trapped for the pet trade or for food?...............................

38. Are there any regulations in place in the communities to control the trapping of birds? Explain………………………………………………………………

Appendix 4.3: GPS coordinates for markets surveyed. Under market name, the city/town in which the market is located is shown in bold.

Region/Province	Market name	Location coordinates	
Greater Accra	**Madina** Market, Accra	W 00º 10"	N 05º 41"
Greater Accra	**Malata** Market, Accra	W 00º 13"	N 05º 33"
Greater Accra	**Kantamanto** Market, Accra	W 00º 13"	N 05º 33"
Ashanti	**Kumasi** Central Market	W 01º 37"	N 06º 42"
Central	**Assin Fosu** Market	W 01º 17"	N 05º 42"
Central	**Twifo Praso** Market	W 01º 33"	N 05º 37"
Central	**Cape Coast** Kotokoraba Market	W 01º 15"	N 05º 07"
Western	**Takoradi** Market	W 01º 46"	N 04º 54"

Chapter 5

SPATIOTEMPORAL CHANGES IN GREY PARROT DISTRIBUTION AND ABUNDANCE IN GHANA

5.1 Abstract

Over the past two decades or more, Grey Parrots may have declined by up to 99% in Ghana, but paradoxically remain reasonably widely distributed in the country. I developed species distribution models (SDMs) with Maxent for the species based on records from the early 1990s (‘historical’) and 2010 onwards (‘current’). Presence records came from 1. Actual field surveys performed by Dändliker (1992) and my own fieldwork in 2012–14; 2. The Global Biodiversity Information Facility (GBIF) based on visiting birdwatchers’ records (current); and 3. Interview data where respondents were asked when they last observed Grey Parrots. Environmental layers were land use, rainfall and rainfall seasonality, EVI, net primary productivity and human population density. Models performed reasonably well, with all but one having AUC > 0.80. Models of historical distribution both from interviews and field surveys showed relatively high suitability for Grey Parrots over much of the study area, but with high suitability in the south and southwest. These distributions matched current suitability based on interviews reasonably well, indicating that Grey Parrots do indeed occur very sparsely (are seen occasionally) over large areas of the country. Distributions based on current fieldwork and GBIF data are much more patchy, with large areas deemed unsuitable, but with high suitability in the extreme south/southwest. Response curves suggested that historically Grey Parrot distribution was correlated most strongly with high rainfall, while current distribution is more closely linked with land use. While SDMs were useful in showing broad suitability

and range contractions at a gross scale, they were less useful in elucidating the factors that control probability of occurrence at a finer scale.

5.2 Introduction

5.2.1 Past and present distribution and abundance of Grey Parrots in Ghana

Parrots generally have brilliant colours and strong 'personalities', and their extraordinary abilities for mimicking human speech and other sounds, as well as exceptional cognitive abilities (e.g. Pepperberg 1994, 2006) afford them very high popular appeal, especially as pets (Collar 1997). They therefore make attractive displays in zoo exhibits and as flagship taxa in biodiversity conservation advocacy (Verissimo et al. 2011). These characteristics make parrots some of the most sought-after animals as pets (Tella and Hiraldo 2014), with huge numbers captured for the international pet trade (e.g. Gastañaga et al. 2011) and a recently highlighted flourishing domestic market in certain range states (Pires 2012). Grey Parrot, especially, remains one of the most traded species internationally (Marsden and Royle 2015).

Unsurprisingly, Grey Parrot populations have undergone massive declines in many parts of their range including Cote d'Ivoire, Ghana, Nigeria, and parts of Cameroon, Democratic Republic of the Congo (DRC), Republic of Congo as well as other countries further east (Martin et al. 2014, Marsden et al. 2015). Recent surveys in Cameroon—where the species was once widely very common and had high population densities—show that numbers have declined drastically or are absent altogether in some areas, although strongholds remain (Tamungang and Cheke 2012). The island of Príncipe, located off the Gulf of Guinea, also holds high population densities in suitable habitat (Marsden et al. 2015). Apparently thriving urban populations of Grey Parrot also occur in parts of the range (e.g. Irumba 2013, Twanza and Pomeroy 2011, Martin et al. 2014).

Grey Parrots originally inhabited nearly the whole of Ghana’s high forest zone (HFZ), and occurred over some 75,000 km^2 of forest. This area encompassed the whole of the Western and Central Regions of the country, most of Ashanti Region and the semi-deciduous forest sectors of southern Brong-Ahafo Region, the western part of the Eastern Region, and parts of the Greater Accra Region (Bannerman 1931, Bouet 1961). There are no records of naturally occurring populations of Grey Parrot in the Volta Region of (easternmost) Ghana—an area that had ostensibly viable habitat for the species—but it reportedly inhabited riverine forests of higher latitude in the country (Dändliker 1992). There were concerns about potential population declines in the Grey Parrot during the 1940s, but large flocks/roosts of 500–1,000 birds persisted (Grimes 1987). Larger flocks of 2,000–3,000 individuals were still observable four decades on (1988) in parts of the species’ area of occupancy in Ghana (Dändliker 1992).

Sixty Grey Parrot roosts/roost areas were known across the forest zone of Ghana by 1992, although not all may have been active at any one time. However, roosts are normally used repeatedly over time. Three of these roosts held 700–1,200 Grey Parrots at the time (Dändliker 1992). Ecological surveys in 28 forest reserves conducted between June 1995 and August 1996 recorded only 87 groups of Grey Parrot during the entire survey period in ‘more than 20’ of the surveyed protected areas (Ntiamoa-Baidu et al. 2000). More recently (December 2008–January 2009), 3–5 day surveys in eight of Ghana’s forest reserves yielded only a total of nine Grey Parrots in six of the surveyed reserves (Dowsett-Lemaire and Dowsett 2014). However, the largest flock size of Grey Parrots in recent years was a group of 38 birds recorded in 2007 at one of Dändliker’s three former ‘big’ roosts (Dowsett-Lemaire and Dowsett 2014). By 2010, Ghana’s forest cover had diminished significantly by a third to approximately 49,400 km^2 (http://rainforests.mongabay.com/deforestation /2000/Ghana.htm). This decline denotes a substantial reduction of Ghana's carrying capacity for Grey Parrots. Grey Parrot populations continue to decrease and the species appears to be locally absent from many previously inhabited areas along the margins of its range in Ghana (Dowsett-Lemaire and Dowsett 2014).

5.2.2 Using SDMs to detect temporal changes in distribution

Species population monitoring is fundamental to determining species' population sizes and trends, factors which, amongst others, are essential for the formulation of appropriate conservation management or policy (e.g. Yoccoz et al. 2001, Witmer 2005). The meagreness of the resources available for conservation action means that such resources must be directed at efforts that maximise conservation returns. It also implies that conservation efforts must often be selectively applied where they are most needed (Brooks et al. 2006, Withey et al. 2012).

Species distribution models (SDMs) are quantitative techniques which associate the incidence of a species at multiple locations with environmental variables at those locations to predict potential distributions based on estimates of the suitability of sites where the species is likely to occur (Wisz et al. 2008, Elith and Leathwick 2009, Duan et al. 2014, Guillera-Arroita et al. 2015). SDMs have been applied widely in various disciplines including ecology, biogeography, biodiversity conservation and natural resource management (Guisan and Thuiller 2005, Newbold 2010, Franklin 2013, Guisan et al. 2013). They have also been applied to studies in terrestrial, freshwater and marine environments, and across species from many biological groups (Elith and Leathwick 2009). The use of SDMs in predicting the potential distribution of species populations is particularly important because knowledge of the areas of occupancy of a species is a prerequisite for focused conservation action (Phillips et al. 2004). Many studies, for example, have examined the effects of climate change on likely range shifts and range contractions in various avifaunal taxa (e.g. Abolafya et al. 2013, Monterrubio-Rico 2015, Stiels et al. 2015). Beyond the climate change approach, Geary et al. (2015) applied scenario-led habitat modelling to citizen science data and showed that such techniques can be useful in assessing the impacts of land use change both on individual species and also on diversity and community measures, or ecosystem services.

In view of the apparent Grey Parrot population declines and range contraction, an assessment of the species' historical and current distribution will be useful for needed conservation efforts. There are many SDM techniques currently available for research. However, Maxent is widely used owing to its better performance in predicting species distributions as compared to other modelling techniques (Elith et al. 2006, Heikkinen et al. 2006, Hernandez et al. 2006, Wisz et al. 2008, Warren and Seifert 2011).

5.2.3 Aim and objectives of study

The aim of this chapter is to use Maxent SDMs to track decadal changes (*circa* 1990–2012) in the distribution of the Grey Parrot across Ghana. To achieve this aim I pursued the following objectives:

1. To build current and historical species distribution models of Grey Parrot using presence point data from different sources (e.g. actual survey records, interviews).
2. To assess distributional changes (shifts) in the Grey Parrot populations over the two decades.
3. To identify the influence of environmental predictors on distributions and distributional changes over time.

5.3 Methods

5.3.1 Study area

The general study area encompassed the high forest zone (HFZ) of south-west Ghana, plus some areas within the drier transition type forests between the rainforests of southern Ghana and the savannas that lie further north in the country (Figure 5.1).

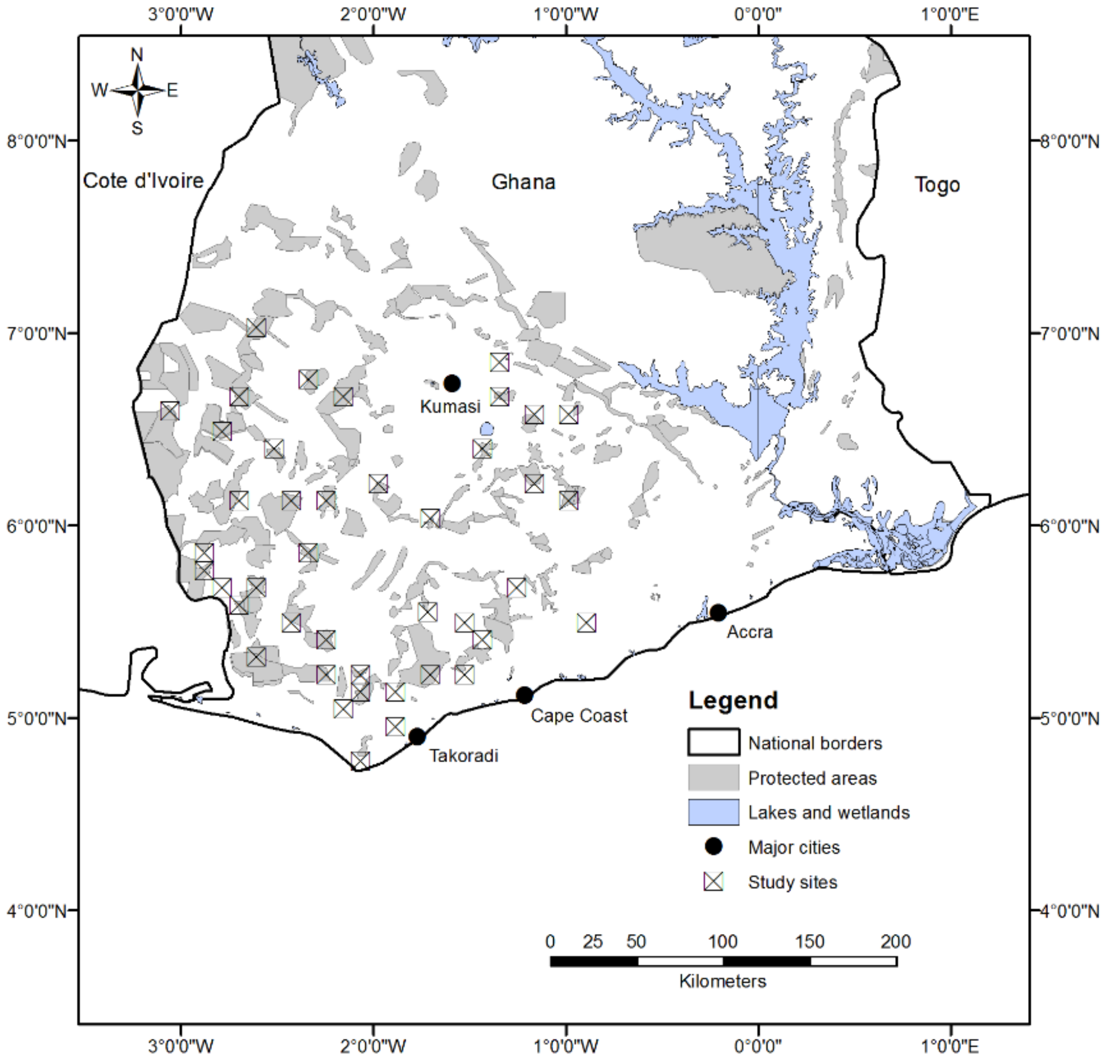


Figure 5.1: Map showing surveyed areas in the high forest zone of southwest Ghana.

The forest zone (~81,000 km^2, Nketiah et al. 2004, Adam et al. 2006), which covers about one third of the country's land area, is distributed over a network of reserved areas comprised of relics of the original forest cover (Nketiah et al. 2004). Hall and Swaine (1981) and Dowsett-Lemaire and Dowsett (2014) provide detailed descriptions of these habitats. Areas surveyed in this study covered small-scale agro-farmland including mature fallows with tall emergent trees and old oil palm *Elaeis guineensis*, large-scale oil palm plantations, primary and secondary forests in protected areas, selectively logged forests, riparian forests, swampy habitats dominated by bamboo (various genera) and raffia palm *Raphia* spp., and the peripheral habitats of rural settlements.

5.3.2 Acquisition of Grey Parrot presence locality datasets

For the purposes of data analyses, georeferenced Grey Parrot presence localities were acquired for two time scenarios, namely 'current' and 'historical'. The current scenario is defined as the distribution of all parrot presence point records obtained for the five-year period between 2010 and 2014, whereas the historical scenario is defined as the distribution of presence localities for the period 1989 to 1993. Datasets for the current scenario were acquired through a combination of ecological field surveys, data from field interviews, records from both the grey literature and published sources, and data queries to the Global Biodiversity Information Facility (GBIF, http://www.gbif.org/). The GBIF is an internet-based international open data resource that facilitates access to data about species on a global scale (e.g. Faulkner et al. 2014, Ficetola et al. 2015). Grey Parrot presence points for the historical scenario were obtained from GPS coordinates recorded from actual visits to the locality descriptions in Dändliker (1992). GBIF did not yield any Grey Parrot locality data for the historical scenario, as none of the records in the database met the temporal definition of the scenario. However, it provided enough data that complemented the species presence records from field surveys (*sensu* Snäll et al. 2011).

5.3.2.1 Ecological field surveys of Grey Parrots

To acquire Grey Parrot presence localities, ecological surveys were conducted over an area of ~70% of the 75,000 km^2 historical range of the species within Ghana, in areas of the west and southwest with the highest potential for still holding the populations of the species. The general study area was partitioned into a grid of 10 km × 10 km cells and a sample of 42 cells was selected, not randomly, but to maximise the probability of encountering Grey Parrot populations (Figure 5.1). This approach was based on historical records of known localities of the species and the presence of considerable forest cover.

Each cell was monitored for periods of 3–5 days, between April 2012 and June 2014, with parrot surveys conducted on each day between 05h45 and 11h00. Surveys covered all habitat types and were conducted by walking along hunter or farmer footpaths and along drivable pathways linking villages and/or towns. Survey routes were trekked in the company of a local guide, and all individual Grey Parrots observed visually or aurally along the route, perched or in flight, were recorded. The directions of flight and GPS coordinates for each observation were also recorded at the point of detection. On some days additional long watches were conducted from vantage positions—mainly locations of higher elevation overlooking a forest canopy, or plain patches of considerable size surrounded by forest—between 16h00 and 18h00. These observations were timed to coincide with the periods of afternoon flight towards overnight roosts (Wirminghaus et al. 2001, Amuno et al. 2007).

Furthermore, surveys were conducted in the vicinity of previously recorded Grey Parrot roosts in Ghana. Between December 1991 and January 1992, Dändliker (1992) identified 60 roosts/roost areas, based on local knowledge of parrot trappers and field staff of the Ghana Wildlife Division. The researcher and his aides visited 22 of these roosts/roost areas but actually counted parrots at only 15 of them. In this study, repeat surveys were conducted in the vicinity of 42 of the 60 historical roosts/roost areas, including those visited by Dändliker. Roost areas were sought for periods of 1–2 days, following Dändliker's descriptions of locations. Former trappers or other knowledgeable local people—including three former trappers who assisted Dändliker over two decades earlier—provided guidance to the known roosts/former roost sites and/or potential alternative roost/aggregation areas.

5.3.2.2 Interviews on local knowledge of Grey Parrots

Questionnaire interviews were conducted in all the study cells and roost areas surveyed to obtain information about local people's knowledge of Grey Parrots and to investigate the presence of the species. The mean number of interviewees per cell/roost area was 17 ± 10 SD (range 3–45). On arrival at a village in a study cell or roost area, the leadership was informed about the study and permission sought to conduct surveys in the area. Together with a dedicated field assistant, we would walk around the village and interview any residents willing to respond to a set of questions from a prepared questionnaire. During the conduct of parrot surveys, the field assistant occasionally interviewed respondents in the forest or in farmland whenever the opportunity arose. A principal component of the questionnaire was to ask interviewees the last time they saw a Grey Parrot in the area.

Although not all interviewees answered every question, a total of 906 people were interviewed within squares and roost areas. The overwhelming majority (97%) were male, 87% were aged 30 years or more and 52% were over 40 years old. The majority (92%) of respondents had lived in their communities for over 10 years, and 85% were farmers. Just 0.2% were 'professional' hunters, although 1% gave hunting as a secondary occupation.

5.3.3 Environmental variables

Of a suite of candidate environmental predictors available for modelling, only six were used for the construction of the Maxent models (Table 5.1). A small number of predictor variables were applied to avoid model over-parameterisation and to ensure high levels of model accuracy (Warren and Seifert 2011, Novaes e Silva et al. 2014). However, the overriding factor in selecting these variables was their ecological relevance to the Grey Parrot (see Elith et al. 2006, Phillips et al. 2006).

Table 5.1: Environmental variables used for model construction. †: Land cover types originally had resolutions of 0.25 and 0.50 km^2, respectively, but were both converted to 1 km^2 pixels.

Variable	Source and detailed description
Climate	http://worldclim.org
Annual rainfall (BIO12)	Hijmans et al. 2005
Seasonality of rainfall (BIO15)	Hijmans et al. 2005
Habitat	https://lpdaac.usgs.gov
Land cover types†	Friedl et al. 2010
Enhanced vegetation index	Solano et al. 2010
Net primary productivity	Heinsch et al. 2003
Anthropogenic	http://www.ciesin.columbia.edu/data/gpw-v4/
Human population density	

Annual rainfall and its seasonality were obtained from the freely accessible WorldClim-Global Climate Data repository, whose resources have been widely used for ecological modelling (http://www.worldclim.org/). The repository holds a set of global climate layers (climate grids) at approximately one square kilometre spatial resolution (pixel size) (Hijmans et al. 2005). Land cover types, enhanced vegetation index (EVI) and net primary productivity (NPP) were obtained from the MODIS website (https://lpdaac.usgs.gov). For the land cover types, a categorical layer of four vegetation classes was reclassified from the 17-class International Geosphere-Biosphere Programme classification system (IGBP, Loveland and Belward 1997, Friedl et al. 2010). The four vegetation classes were as follows: 1 = evergreen + deciduous forest, 2 = open + closed shrubland, 3 = cropland + natural vegetation and cropland, and 4 = urban + built-up area. EVI is a global-based vegetation index for monitoring terrestrial photosynthetic activity on the surface of the earth (Matsushita et al. 2007, Solano et al. 2010). Similarly, NPP is a measure of the rate at which all plants in an ecosystem produce net useful chemical energy and in itself can be a measure of habitat suitability (Heinsch et al. 2003). As a measure of anthropogenic pressure on the environment, data for human population density estimates in persons per square kilometre were obtained from the Gridded Population of the World, version 4 (GPWv4) dataset (http://www.ciesin.columbia.edu/data/gpw-v4/). All environmental data were re-engineered in ArcMap 10.2.2 to produce data layers of identical projection, spatial extent, grid cell size and alignment in order to ensure consistency with the requirements of the Maxent software (Phillips undated, Elith et al. 2006).

5.3.4 Model development and evaluation

Grey Parrot distribution models were developed for multiple case studies. For the current scenario, case studies included presence locality datasets from 1: field surveys (this study), 2: GBIF database, 3: combination of field surveys (this study) and GBIF database, and 4: interviews. Models for the historical scenario were developed from georeferenced presence locality datasets obtained from 1: visits to sites where Dändliker (1992) recorded Grey Parrots 1991/1992 and 2: all interviewee locations where Grey Parrot was previously present. I assumed that all current Grey Parrot localities have previously held populations.

Version 3.3.3k of the Maxent software was used to develop the SDMs (see http://www.cs.princeton.edu/~schapire/maxent/). The choice of a presence-only analytical approach was made for two reasons. First, the Grey Parrot makes nomadic movements within the forest zone in response to the availability of food resources (Fry et al. 1998, Collar et al. 2015), and absence from surveyed sites did not necessarily imply unsuitability of such sites as potential habitat. Second, the Grey Parrot has suffered drastic population declines (Dowsett-Lemaire and Dowsett 2014, Martin et al. 2014, Marsden et al. 2015) and hence may not be occupying all of its potential habitats, despite their suitability (Cianfrani et al. 2010). Absence from surveyed sites may therefore be related to other factors than habitat relationships (Geary et al. 2013).

Following contemporary trends in the application of Maxent, with cues from recent findings (e.g. Merow et al. 2013, Elith et al. 2011), the models were run with a combination of default and alternative settings. To enable an assessment of model robustness for each species, 20 replicate runs were performed on the data with 75% of the presence records selected randomly to train the model, and the remainder to test its predictive performance. The subsample replication option was selected, with a maximum of 5,000 iterations per replicate run, 10,000 maximum background points, and a convergence threshold of 0.00001. Even though some authors have proposed the application of species-specific values for model regularisation (e.g. Anderson and Gonzalez 2011, Warren and Seifert 2011), the default value of 1 is adequate for most presence-only datasets (Phillips et al. 2004, Phillips and Dudik 2008) and is still widely used (e.g. Abolafya et al. 2013). To minimise the effects of sampling bias, Maxent was instructed to apply one presence record per cell by activating the 'remove duplicate presence records' tab.

To evaluate the performance of the model for each species, the receiver operating characteristic (ROC) was used. This approach assesses the performance of a Maxent model using the area under the ROC curve (AUC, area under curve), and is a widely used measure of model performance (Elith et al. 2006, Wisz et al. 2008, Vidal-Garcia and Serio-Silva 2011). The AUC represents the probability of ranking a presence locality above a background locality (pseudo-absence) when both are chosen at random (Phillips et al. 2006, Phillips and Dudik 2008). Models with AUC values of 0.5 indicate a prediction no better than random whereas a value of 1 is a perfect prediction (Elith et al. 2006, Phillips and Dudik 2008, Abolafya et al. 2013). The contribution of each environmental variable to models was assessed by performing a jackknife test in Maxent, which determines the influence of each variable on model gain by excluding it or applying that variable alone in analyses (Elith et al. 2006, Vidal-Garcia and Serio-Silva 2011).

Distributional differences both across time and between different methods or case studies were assessed visually from the Maxent output maps and contributions of predictor variables and shapes of responses examined.

5.4 Results

5.4.1 Model performance

The Maxent distribution models performed well. Values of AUC for the predicted distributions of the Grey Parrot for all case studies of both historical and current environmental model scenarios are evidently much greater than expected for random events (range = 0.77–0.88; Table 5.2). Distribution models for three case studies predicted high probabilities of occurrence (PoOs), with AUC values ranging from 0.87–0.88 (Table

5.2). All case studies except 'Interviews-recent sightings' (AUC = 0.77) had AUCs greater than 0.80.

Table 5.2: Number of presence records used in the Maxent models and mean Test AUC values (n = 20) with standard deviation for each case study. AUC values are arranged in decreasing order for easy assessment.

Case study	No. of records	AUC (mean ± SD)
Interview (all time)	95	0.88 ± 0.02
Dändliker	39	0.87 ± 0.03
Current survey	16	0.87 ± 0.05
Current survey + GBIF	33	0.84 ± 0.07
GBIF	19	0.82 ± 0.09
Interview (recent sightings)	70	0.77 ± 0.04

AUC values returned from ROC plots for Maxent training data for the 20 replicate runs showed very little variation in the majority of case studies. Five of the six models (83%) had median AUC greater than 0.90 (Figure 5.2). Test AUC values showed acceptable degrees of variation, with models for GBIF and GBIF+Current survey case studies showing the highest degree of variation.

5.4.2 Predicted distributions and probabilities of occurrence

The historical and current distributions of the Grey Parrot are shown in Figure 5.3. A comparison of the historical and current distributions indicates appreciably lower probability of occurrence (PoO) in the latter over large parts of the species' range in Ghana. However, both historical and current scenarios show areas of high PoO in the southwest of the range. From the current scenario (Figure 5.3 c-f), higher latitudes over the southwest have appreciably lower PoO. The historical scenario shows areas of relatively high PoO outside of the southwest, which occur in the northeast and northwest of the range. The prediction from interview data for the current scenario (Figure 5.3 e) is similar to those of the historical scenario, but shows a relatively higher PoO in comparison to its counterparts.

Model predictions for the historical scenario, i.e. both interview and Dändliker case studies, match closely, showing areas of high PoO in the southwest, northeast and regions around the northwest of the range. There are, however, regions of low PoO in the central expanses of the range. Looking across different case studies for the current scenario, field survey and GBIF predictions match fairly closely. Both case studies identify distributional hotspots (regions with relatively high PoO) in the southwest of the range. However, the hotspots for the field survey case study are skewed towards the southwestern corner of the range, whereas those of the GBIF identify this area but also areas to the east of the southernmost region of the range (Cape Three Points Forest Reserve). A striking feature of the GBIF case study is an area of low PoO in the southwest, just north of Ankasa Resource Reserve and south of Sui River Forest Reserve (see Figure 5.1 for protected areas). In contrast, the interview case study for the current scenario predicts a fairly even PoO across the landscape, with a V-shaped ‘hotspot’ stretching from Cape Three Points northwards.

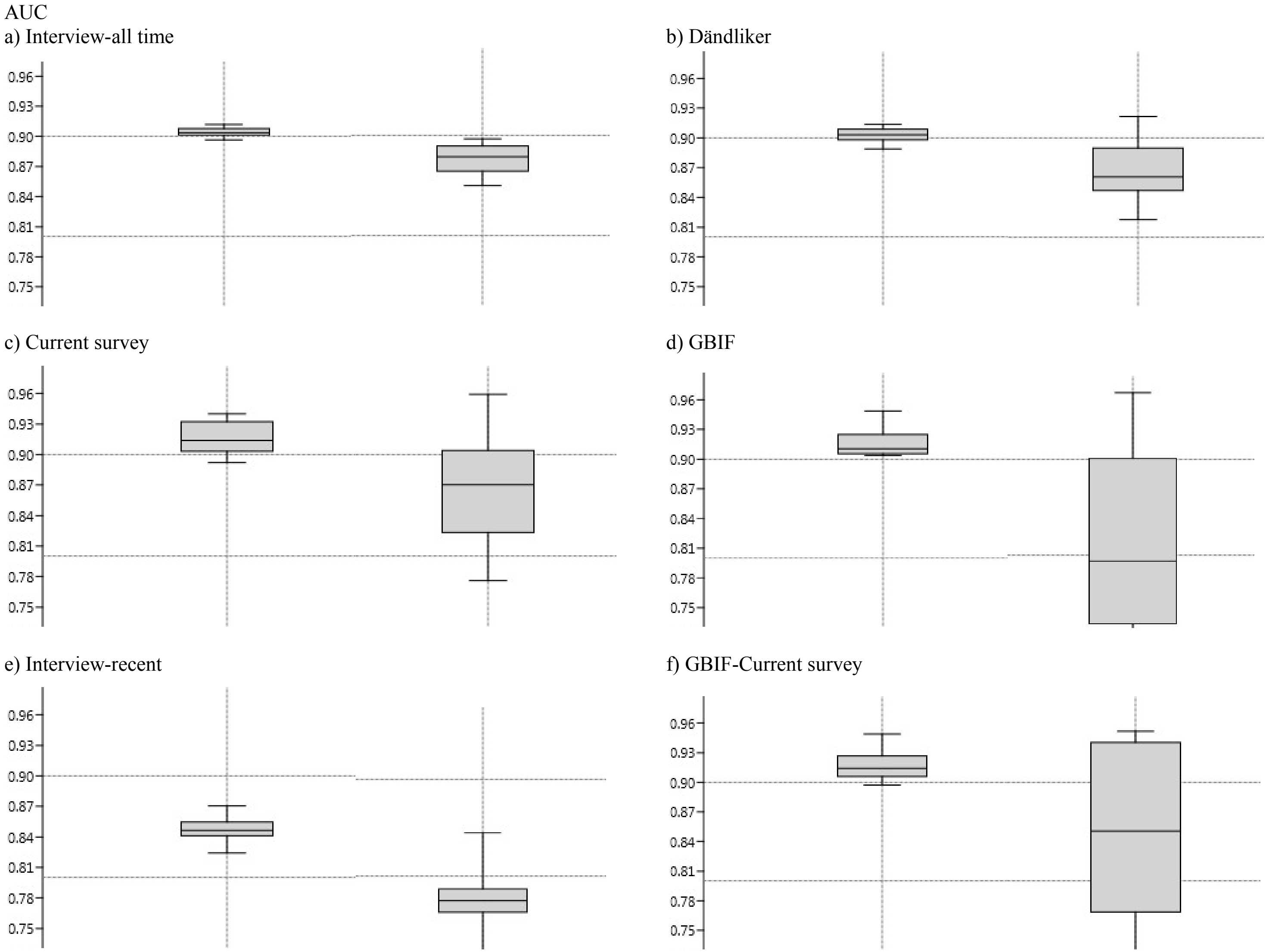
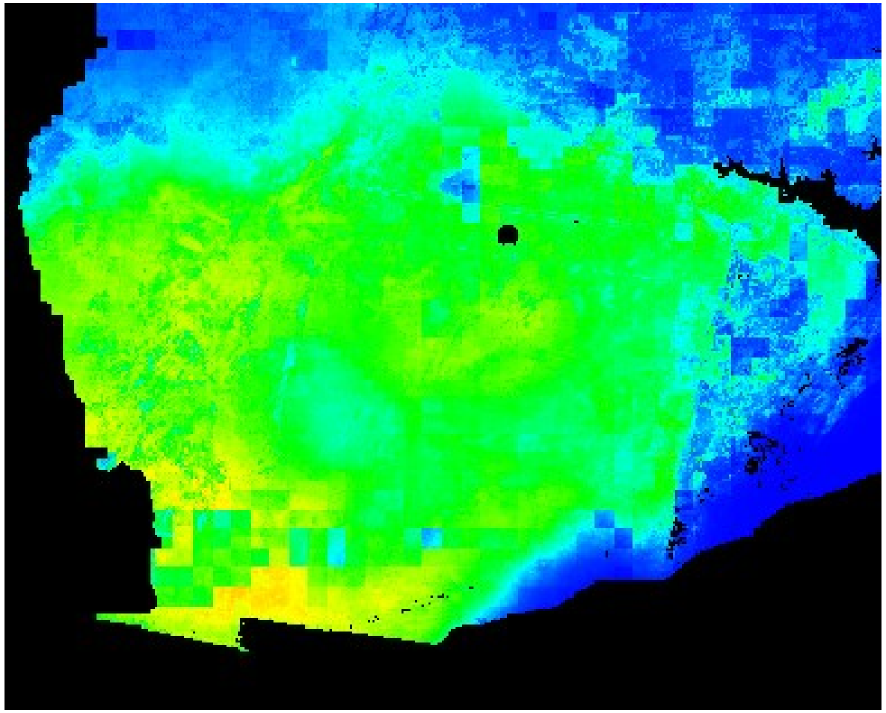
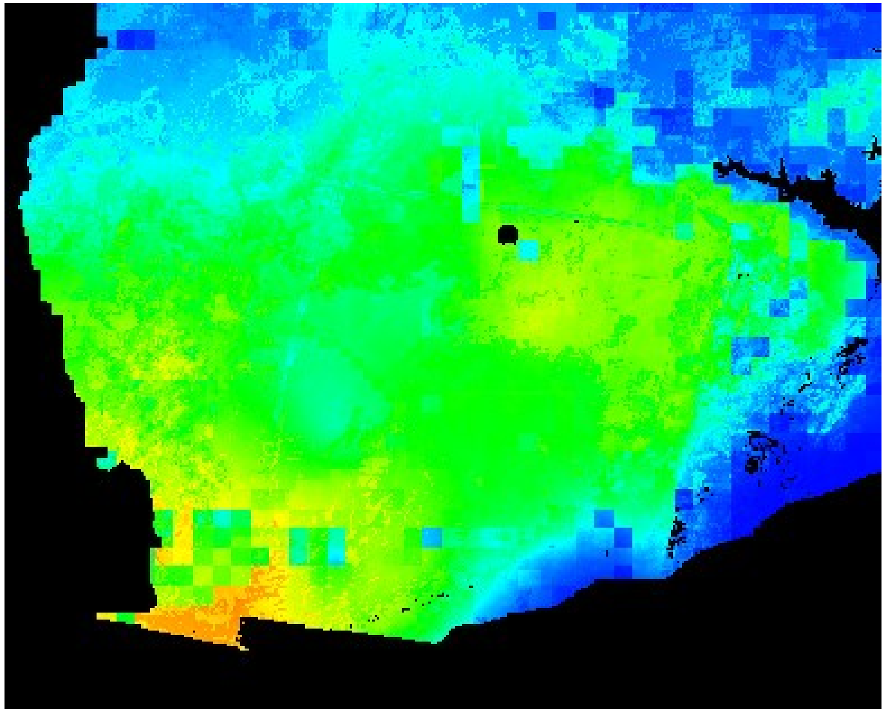


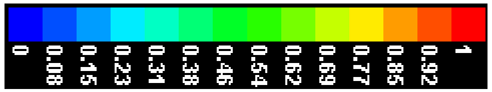
Figure 5.2: Box plots showing Maxent model performance based on training (left bar) and test (right bar) AUC values for 20 replicate runs. The horizontal line in a box shows the median AUC, the box shows quartiles and the whiskers represent 5–95% of AUC values.





a) Interview (all time)

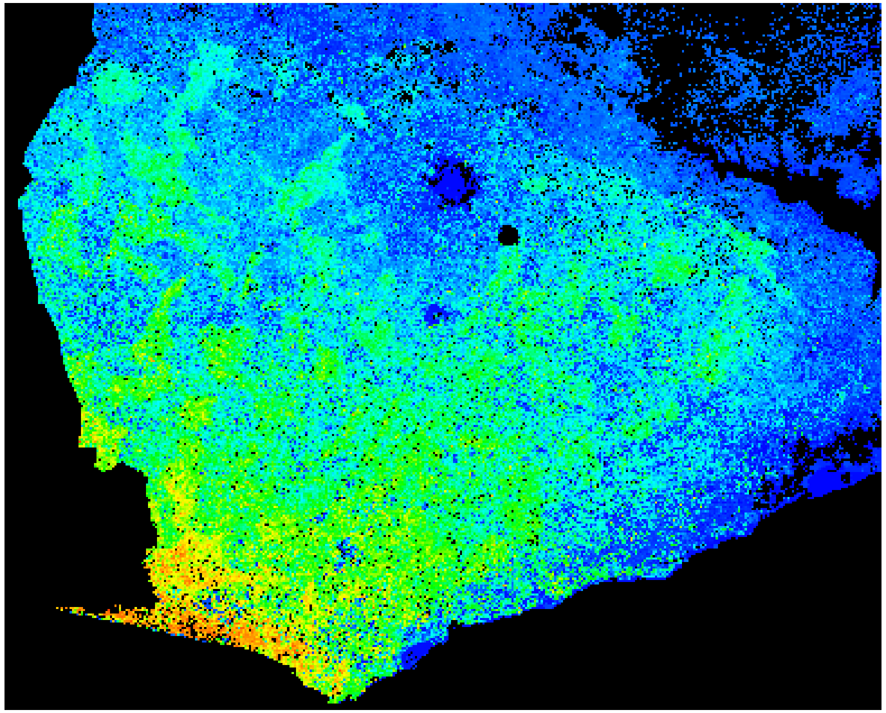
b) Dändliker



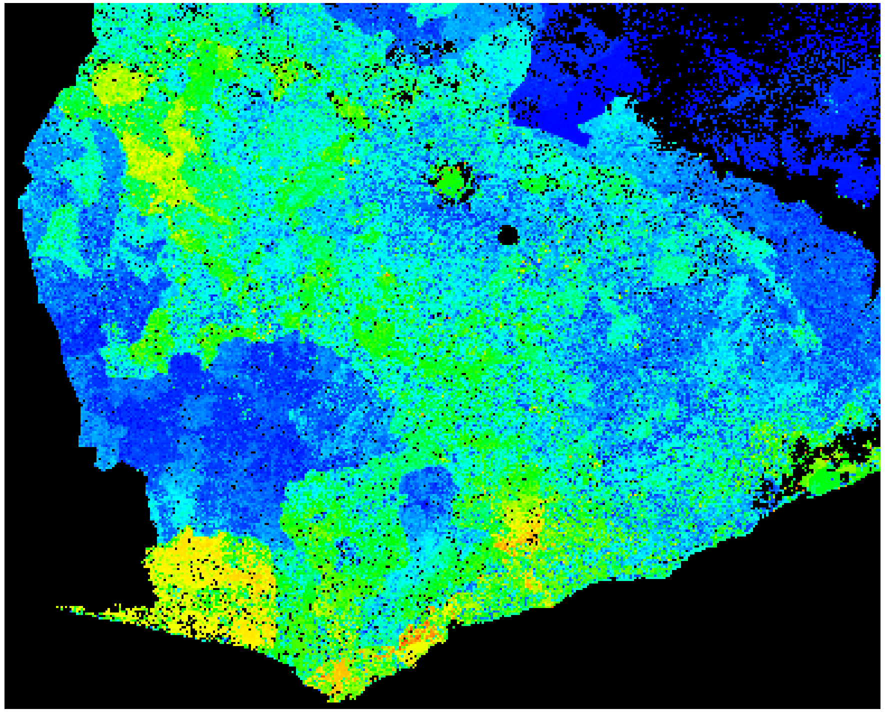
Scale of probabilities for Maxent distributions

Figure 5.3 Maxent output maps showing historical (a-b) and current (c-f) distributions of Grey Parrot. The current scenario is defined as the distribution of all parrot presence point records obtained for the five-year period between 2010 and 2014, whereas the historical scenario is defined as the distribution of presence localities for the period 1989 to 1993.

Figure 5.3 Continued.

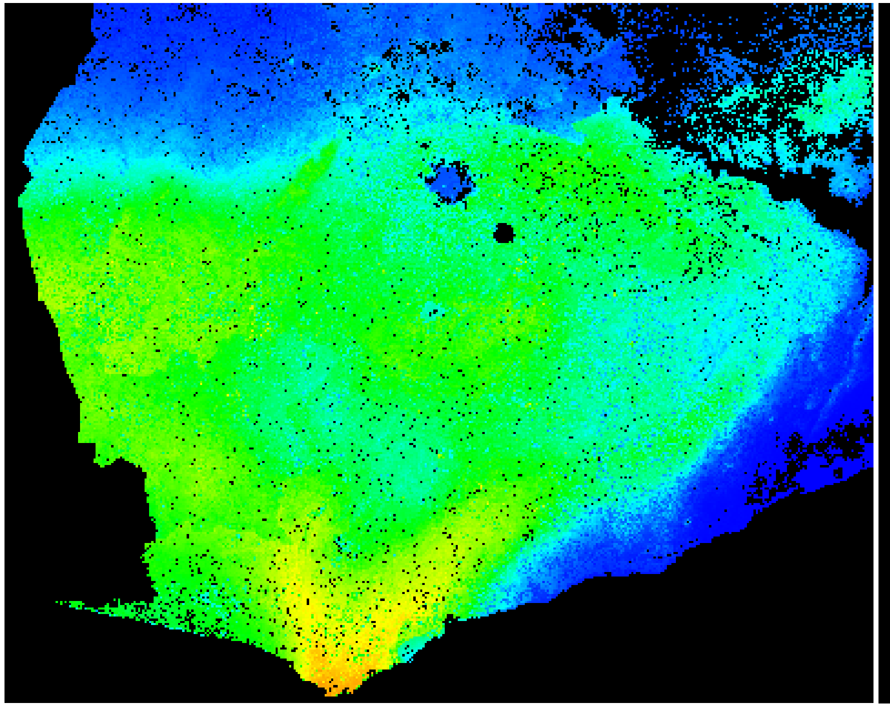


c) Current survey

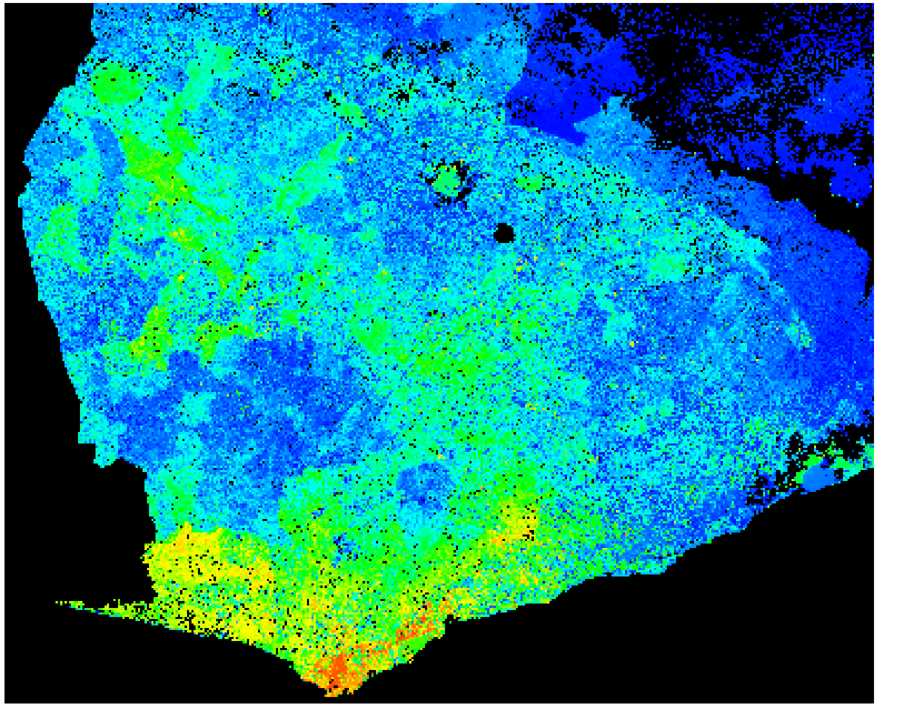


d) GBIF

Figure 5.3 Continued.



e) Interview (recent sightings)



f) Current and GBIF (combined)

5.4.3 Distributional shifts and range contraction

The predicted spatial distributions of Grey Parrot for both historical case studies (Interview and Dändliker datasets; Figure 5.3) are very similar. Both predictions have areas of high PoO in the extreme southwest of the HFZ, although the Dändliker dataset has areas of comparatively higher PoO. The historical predictions also compare closely with that of the Interview case study for the current scenario, but with the area of high PoO shifted east in the latter. Predicted distributions for the remaining case studies for the current scenario show marked range contractions. The current survey case study shows a significant loss of suitable habitat north and east of the range, with areas of high PoO restricted to the southwestern corner. The combined Current and GBIF dataset, however, shows similar loss of suitable habitat, but with very high PoO at the southernmost part of the range and with moderately high areas of PoO further east and west.

5.4.4 Main environmental predictors of distributions and distributional changes

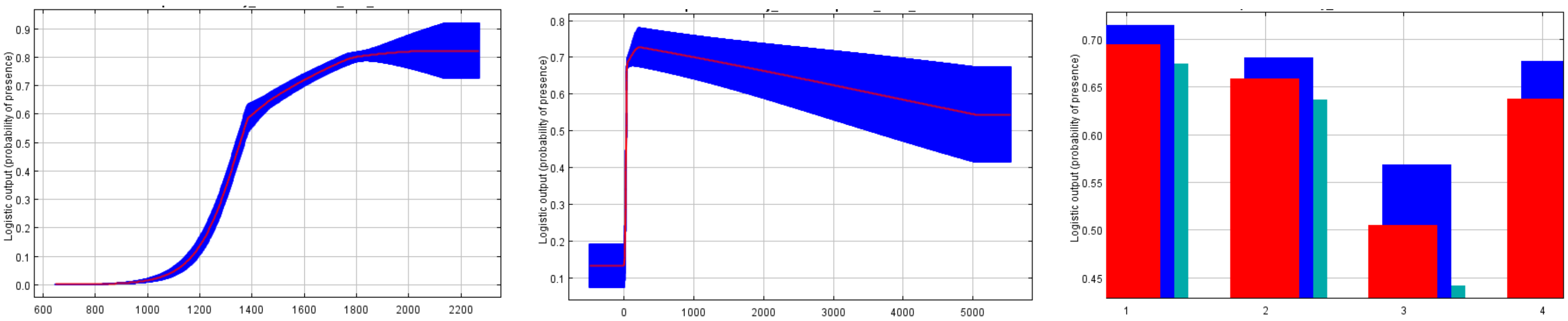
In all case studies, the top three environmental variables contributed between 77 and 97% to model development (Table 5.2). Annual rainfall, land cover and NPP were the foremost variables that contributed to models. Annual rainfall was the top contributory variable for the two historical models, accounting for 58–68% of AUC in both case studies. Percent contribution by the topmost variables for current case studies showed greater variation (range = 28–78%).

The historical case studies had similar models: their annual rainfall response curves are sigmoid in shape, with peak PoO (0.82–0.95) around 2,000–2,100 mm (Figure 5.3a and b). Increasing human population density did not change PoO significantly, but tended to have a negative effect. For current case studies, the land cover categories with the highest percent contribution were shrub land and urban areas (Figure 5.3).

Table 5.3: Top three predictor environmental variables contributing to the prediction of Grey Parrot distribution in Ghana for various case studies. Figures in parentheses represent the percent contribution of each of the first three predictor variables to model construction.

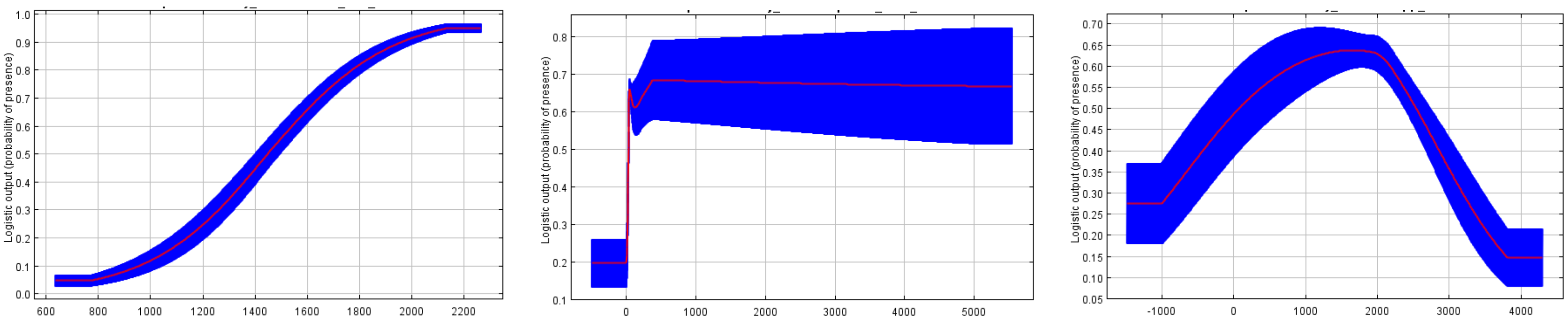
Scenario	**Variable 1**	**Variable 2**	**Variable 3**	**Total % contribution**
Interview (all time)	Annual rainfall (57.5)	Population density (18.4)	Land cover type (15.7)	91.6
Dändliker	Annual rainfall (67.8)	Population density (21.0)	NPP (3.8)	92.6
Current survey	Land cover type (42.9)	Annual rainfall (32.3)	NPP (23.3)	98.5
Current and GBIF (combined)	NPP (38.9)	Land cover type (25.6)	Rainfall seasonality (12.7)	77.2
GBIF	Land cover type (28.3)	Population density (28.3)	NPP (27.9)	84.5
Interview (recent)	Annual rainfall (78.3)	NPP (9.4)	Rainfall seasonality (9.3)	97.0

Interviews (all time): 57.5, 18.4, 15.7



Annual rainfall | Human population density | Land cover types

Dändliker: 67.8, 21.0, 3.8

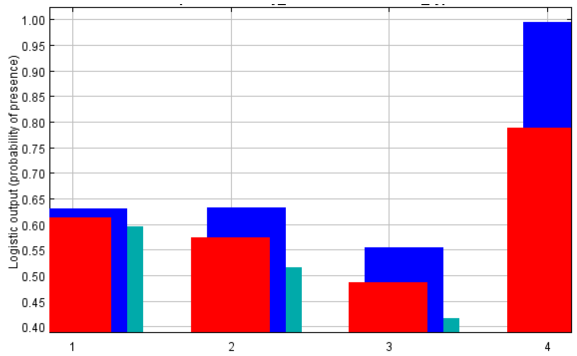


Annual rainfall | Human population density | Net primary productivity

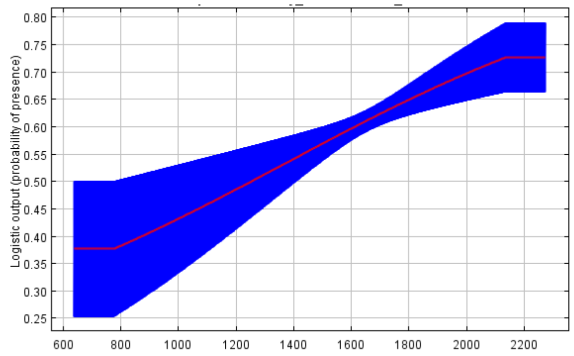
Figure 5.4: Graphs showing trends in how probabilities of presence varied with environmental variables during model development. Red lines indicate mean values for the 20 replicate model runs for each case study, whereas blue shading represents the range of probabilities from each replicate.

Figure 5.4.2 continued.

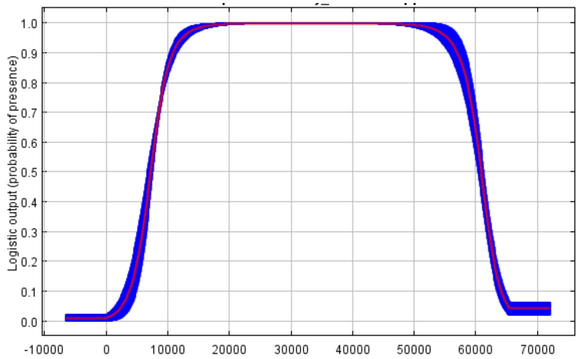
Current survey: 42.9, 32.3, 23.3



Land cover types

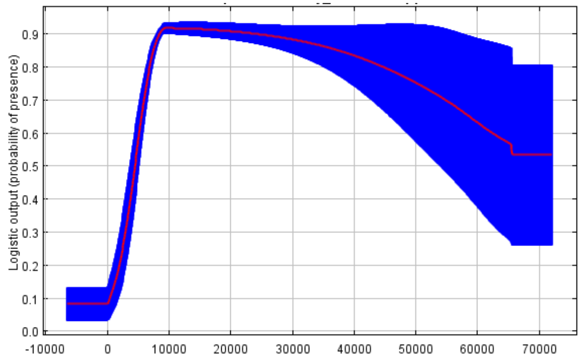


Annual rainfall

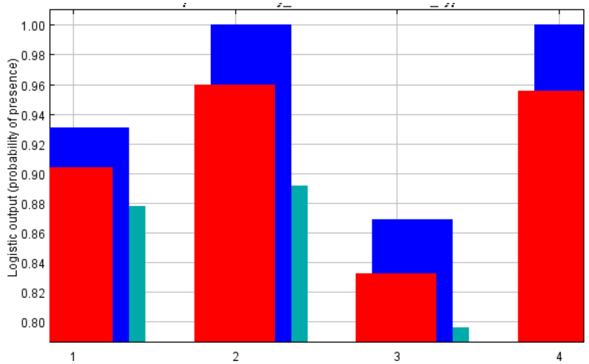


Net primary productivity

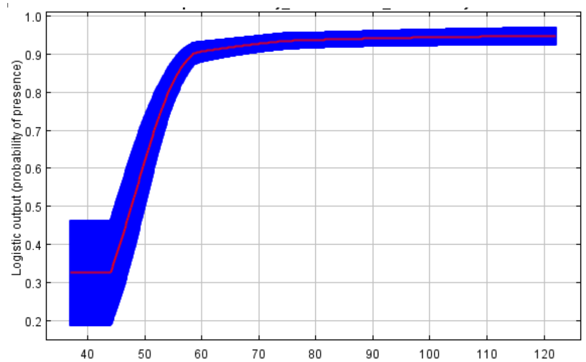
Current survey and GBIF (combined): 38.9, 25.6, 12.7



Net primary productivity



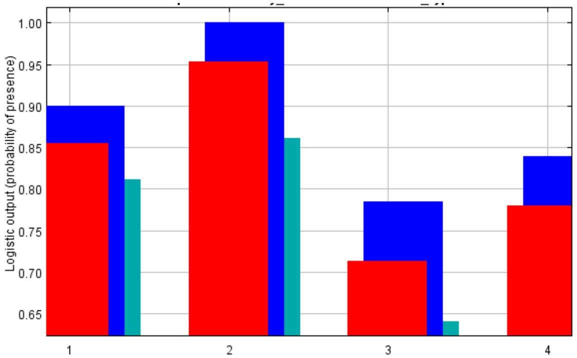
Land cover types



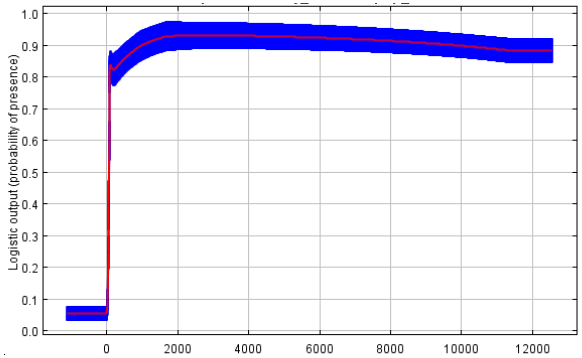
Rainfall seasonality

Figure 5.4.2 continued.

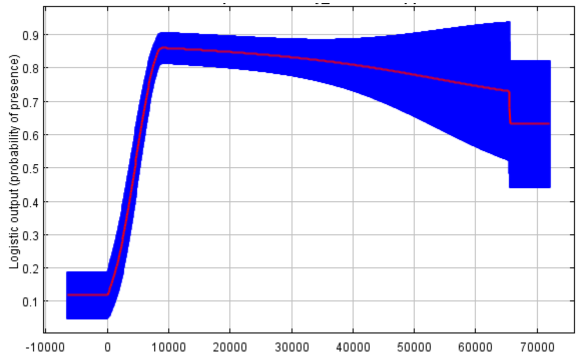
GBIF: 28.3, 28.3, 27.9



Land cover types

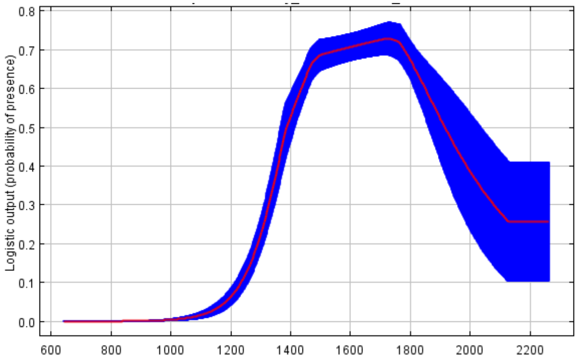


Human population density

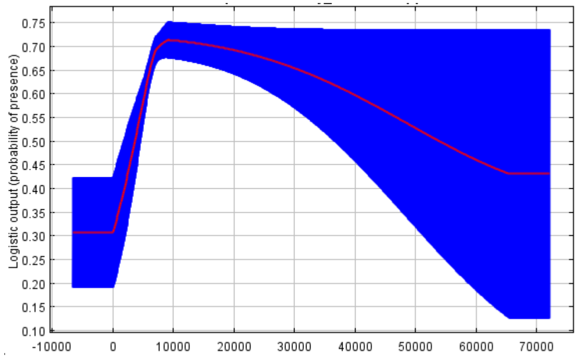


Net primary productivity

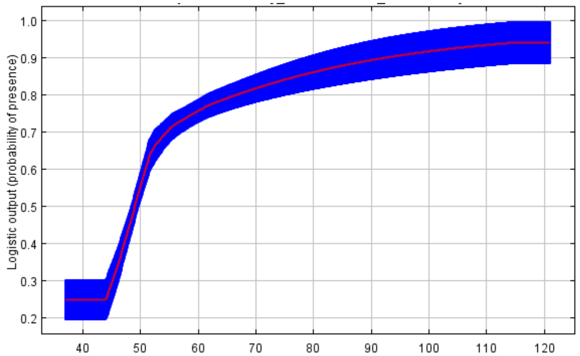
Interview (recent): 78.3, 9.4, 9.3



Annual rainfall



Net primary productivity



Rainfall seasonality

5.5 Discussion

Comparing historical and current model methods, the distribution of Grey Parrot in Ghana is predicted to have declined severely over the last 24 years (at least since 1992). The predictions of this study largely agree with the recently published Ghana bird atlas (Dowsett-Lemaire and Dowsett 2014), whose findings indicate that the Grey Parrot is no longer present in many areas on the margins of its range. Many interior parts of the range predicted to have very low PoO are also reported to have suffered marked population declines over the past few decades (Dowsett-Lemaire and Dowsett 2014, Martin *et al*. 2014, Marsden *et al*. 2015). It is often the case that species population declines co-occur with localised lack of occupancy in some areas within a species' range (Gaston *et al*. 2000). The predicted range contraction and very low PoO at some interior parts of the range (probably indicative of major population declines)—over a time-span a little more than the past two decades—appears to reflect a problem across the entire African range of the Grey Parrot. Using different methods, similarly severe population declines have been reported elsewhere in the range, including eastern Côte d'Ivoire, where no parrots were recorded during recent surveys (Marsden *et al*. 2015). Populations have suffered similarly severe declines in Nigeria, where the species has become highly fragmented within protected areas (Martin *et al*. 2014). The situation in Nigeria may be similar to that of Ghana, as the species was unrecorded in many parts of the Nigerian range in the early and late 2000s (McGowan 2001, Olmos and Turshak 2009). Appreciable population declines have been noted over the last few decades in many areas in a number of Central and Eastern African countries, e.g. Cameroon (Tamungang and Cheke 2012), Democratic Republic of the Congo (DRC) (Hart 2013), Uganda (Amuno *et al*. 2007) and Kenya (Martin *et al*. 2014).

The distribution of Ghana's Grey Parrot populations has contracted (or changed) over the last two decades. Although the AUC values were relatively high—which is indicative of good performance by the Maxent models—the individual case studies (Maxent models using different datasets) differed significantly at the local scale regarding the predictions of areas of high PoO. Admittedly, differences in the precision of SDM predictions based on different datasets for the same species do occur (e.g. Lentini and Wintle 2015), often due to data heterogeneity (Sarda-Palomera et al. 2012). However, the observed decadal contraction in suitable habitat for the Grey Parrot is a true reflection of the status of the species' populations in Ghana. The species has not been recorded in many areas within its range, including protected areas, for many years (Dowsett-Lemaire and Dowsett 2014).

Patterns of predicted distribution were different between datasets, as can be the case when there is variation in sample sizes and survey methodologies (Sarda-Palomera et al. 2012). The Current field survey dataset tended perhaps to overpredict the probability of occurrence for Grey Parrot in the southwest. Current field survey and GBIF predictions were more similar to each other but still differed at the local level. These differences are ostensibly due to the concentration or 'spatial clumping' of presence records in some areas. For example, the GBIF dataset predicted high probability of occurrence in the northwest of the range, presumably due to a few records from well-watched presence localities (e.g. Snäll et al. 2011, Sarda-Palomera et al. 2012). The combined Current survey and GBIF dataset was perhaps the best in identifying southwest Ghana as the core inhabited area as it maximises sample size of presence points, and perhaps characterises better the presence of birds in the extreme south, an area not so well characterised as of high PoO by the Current survey dataset alone.

The two historical models, as well as that of the GBIF, predicted reasonably high PoO across areas northeast and northwest in addition to the ‘strongholds’ in the southwest. This might be true for the historical cases when the Grey Parrot occurred across the whole of the HFZ two decades ago (Dändliker 1992), but the prediction from the ‘GBIF only’ dataset (current scenario) is misleading as the species has not been sighted in most of those areas for many years (e.g. Bia National Park and Resource Reserve: Dowsett-Lemaire and Dowsett 2014, Holbech 2014, Martin et al. 2014). This calls into question how precisely SDMs predict occupancy for rare and patchily distributed species such as Grey Parrot whose populations are impacted synergistically by ‘complex’ stressors e.g. habitat change and direct exploitation acting concurrently.

Unlike for most of the large frugivores in *Chapter 3*, identification of the influence of environmental predictors on the distribution of the Grey Parrot was not straightforward, especially with the use of different datasets. However, annual rainfall, land cover type and net primary productivity (NPP) appear to be the major environmental factors responsible for the distribution of Grey Parrot in the HFZ of Ghana. Annual rainfall was very important for the distribution of the species over two decades ago, with areas of relatively high rainfall (2,000–2,100 mm per year) predicted to be most suitable. For the current scenario, land cover type showed an elevated importance in predicted Grey Parrot distributions as compared with other models, especially the historical ones. This observation may be explained by the increasing destruction of suitable Grey Parrot habitats (e.g. Dowsett-Lemaire and Dowsett 2014, Holbech 2014). Probability of occurrence for Grey Parrot populations was not greatly affected by increasing human population density. This may explain why healthy populations of the species continue to thrive in ‘safe’ urban areas with seemingly suitable habitat (see Twanza and Pomeroy 2011, Irumba 2013). NPP is a measure of the availability of food resources (or energy) in the environment and studies show that species abundance in an area is positively correlated with food availability (Poulin et al. 1993, Wright et al. 1993, Mönkkönen et al. 2006). This is because higher levels of environmental energy yield a larger resource pool, which then sustains more individuals (Pautasso and Gaston 2005). Expectedly, many studies indicate that the abundance of tropical avian frugivores is strongly influenced by fluctuations in the abundance of fruit (e.g. Fogden 1972, Karr 1976, Greenberg 1981, Pavey et al. 2014).

5.6 References

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Chapter 6

CONCLUSIONS AND DISCUSSION: PROSPECTIVE PARROT AND OTHER FRUGIVORE CONSERVATION RESEARCH IN GHANA

6.1 Main aim of the PhD thesis

The aim of this PhD was to assess the historical and current distribution, abundance and ecology of western populations of the African Grey Parrot *Psittacus erithacus* in order to make informed predictions about the sustainability of trade and land-use changes. Relevant data on other large avian frugivores were also collected as an integral part of the study.

6.2 Summaries of main findings

6.2.1 Chapter 2: Frugivore communities and abundance across Ghana

In Ghana, many large avian frugivores face various threats to their survival including habitat loss, hunting and trapping for food and the international pet trade. However, there is little or no precise information on the past or present distribution and abundance of many members of this avian guild. This chapter investigated patterns of frugivore occurrence and abundance across the country. It assessed frugivore diversity in the study area and used Canonical Correspondence Analysis (CCA) to identify the main drivers or environmental gradients influencing bird community make-up. Frugivore species richness varied across study sites from two to 15 species. The most abundant species, African Pied Hornbill *Lophoceros semifasciatus* and African Green Pigeon *Treron calvus*, were recorded in nearly all study sites. The most restricted and rare species included the large-bodied Great Blue Turaco *Corythaeola cristata*, Yellow-casqued Hornbill *Ceratogymna elata* and Black-casqued Hornbill *C. atrata*. The CCA analysis showed that large-bodied hornbills and a few other species tended to occur in areas characterised by large reserved forest with low anthropogenic disturbance. Many large avian frugivores in Ghana are neither common nor widely distributed. The analysis demonstrates the vital importance of large, little disturbed tracts of habitat for this guild.

6.2.2 Chapter 3: Distribution modelling for large avian frugivores across Ghana

The probability of occurrence (PoO) of 15 species of avian frugivore across Ghana was investigated using environmental data as predictor variables. This chapter assessed the individual variables that were the strongest drivers/correlates of current distribution and sought to identify hotspots for frugivore conservation and to guide conservation actions onto appropriate locations. Frugivores showed varying degrees of restriction to Ghana's large forest reserves, with Afep Pigeon *Columba unicincta*, Western Bronze-naped Pigeon *Columba iriditorques*, Great Blue Turaco, Yellow-billed Turaco *Tauraco macrorhynchus*, Black Dwarf Hornbill *Tockus hartlaubi* and Red-billed Dwarf Hornbill *T. camurus* being most strongly limited. Most species had highest PoO in the southwest of the country. The main driver of distribution in the majority of species was land cover type (11/15 species), with forest habitats preferred in 90% of cases as opposed to shrubland, cropland and urban built-up areas. Key sites for conservation of frugivores are the large forest reserves in the southwest of the country. It is therefore crucial that Ghana's forest reserves are adequately protected to ensure that human encroachment and logging are controlled.

6.2.3 Chapter 4: Trade and habitat change virtually eliminate the Grey Parrot from Ghana

The heavily traded Grey Parrot appears to have suffered a catastrophic population decline, yet there is little quantitative data on trends in population sizes over time from anywhere within its huge range. This chapter assessed the species' historical abundance across Ghana, examined targeted searches during 3- to 5-day visits to 42 100-km^2 cells across the country's forest zone, examined repeated counts at 22 parrot roosts first performed two decades ago and gauged around 900 people's perceptions of the decline and its causes. Over 150 days of fieldwork yielded just 32 groups (maximum group size = 12) recorded in 10 cells. Encounter rates averaged 0.15 individuals per hour of targeted search, about 15 times less than those recorded in the early 1990s. Active roosts, i.e. roosts in current use, could not be found, and just 18 individuals were documented in three roost areas that each harboured 700–1200 birds two decades before. Respondents to interviews stressed the significance of very tall trees of commercially important timber species such as *Terminalia superba* and *Ceiba pentandra* for nesting and roosting, and believed that the removal of large trees from farmland (42% of responses) and capture for trade (37%) were the two main causes of the massive decline. Ghana has lost 90–99% of its Grey Parrots since 1992, a time when the population had apparently already been drastically reduced by two decades of very heavy trade. Doubtlessly, away from one or two localities, declines appear to be severe throughout the West African range of *P. erithacus*, as well as the entire range of the Grey Parrot's recently split congener, Timneh Parrot *Psittacus timneh*.

6.2.4 Chapter 5: Spatiotemporal changes in Grey Parrot distribution and abundance in Ghana

The Grey Parrot may have declined by up to 99% in Ghana over the past two decades or more, but the species is still reasonably widely distributed in the country. I developed species distribution models (SDMs) with Maxent for the species using records from the early 1990s ('historical') and 2010 onwards ('current'). I obtained presence records from 1. Actual field surveys performed by Dandliker (1992) and my own fieldwork in 2012–14; 2. The Global Biodiversity Information Facility (GBIF) based on visiting birdwatchers' records (current); and 3. Interview data where respondents were asked when they last observed Grey Parrots. Environmental layers were land use, rainfall and rainfall seasonality, EVI, net primary productivity and human population density. Models performed satisfactorily, with all but one having AUC > 0.80. Models of historical distribution both from interviews and field surveys indicated relatively high suitability for Grey Parrots over much of the Ghanaian range, but with highest suitability in the south and southwest. These distributions closely corresponded with current suitability based on interviews, indicating that Grey Parrots do indeed occur very sparsely over most of the range. Distributions based on current fieldwork and GBIF data are much more irregular, with large areas predicted unsuitable, but with high suitability in the extreme south/southwest. Response curves indicated that, historically, Grey Parrot distribution was associated most strongly with high rainfall, while current distribution is more closely influenced by land use. While SDMs were useful in showing broad suitability and range contractions at a gross scale, they were less clear in clarifying the factors that control probability of occurrence at a finer scale.

6.3 The past, present and future of Grey Parrots in West Africa

Historically, the Grey Parrot had a distribution that covered nearly the whole of Ghana's high forest zone (HFZ) (Bannerman 1931, Grimes 1987, Dändliker 1992). The species had very high population densities, and was a common spectacle in rural areas, with nests and roosts often near and even within villages (Dändliker 1992). It was a common sight to observe hundreds of individual birds in population strongholds owing to their tendency to form large communal aggregations. The African Green Pigeon and African Pied Hornbill remain very common species of relatively high abundance in Ghana's forest zone (e.g. Ntiamoa-Baidu et al. 2000, Dowsett-Lemaire and Dowsett 2014), and historical data from the literature and interviewee accounts indicate that Grey Parrot numbers rivalled closely those of the former species (see Chapter 4). In Ghana, the Grey Parrot used to be revered locally for its mimetic abilities, and is the emblem for a number of traditional authorities. For example, the Agona clan of the Akan tribes of Ghana regard (or regarded) the species as their totem. It was therefore respected, considered sacred and was not killed or eaten (Ntiamoa-Baidu 1995). However, owing to increasing human population, urbanisation and industrialisation, and the introduction of foreign religions, many taboos and traditional practices have largely been eroded, to the detriment of wildlife (Ntiamoa-Baidu 1987).

The Grey Parrot has suffered from a long history of international trade from Ghana, with the 1970s through the 1990s representing the peak period for the exploitation of the species (Ussher 1874, Lowe 1937, Dändliker 1992). The Grey Parrot, together with its congener the Timneh Parrot, has been very popular among pet keepers, and this popularity has unsurprisingly translated into the very large volumes of trade in wild-sourced specimens that have been witnessed over recent decades. Reported trade figures represent legal international trade, but high pre-export mortality (Clemmons

2003, Hart 2013) and illegal trade (Pain et al. 2006, Pires 2012), both inevitably poorly documented and quantified, compound the very dire status of these species. It is incontrovertibly clear from this study that the Grey Parrot is currently very rare across Ghana, and the Timneh Parrot may have suffered a similar fate (Martin et al. 2014, Marsden et al. 2015). The extent of capture and trade in the Democratic Republic of the Congo, for example, is currently believed to be unsustainable (Hart 2013). The situation is similar in Cameroon (Tamungang et al. 2014) and many other parts of the range (Martin et al. 2014). The case of the *Psittacus* parrots is not unique, however; the international illegal parrot trade has been a major contributor to the endangerment of a significant proportion of the world's parrot species (Wright et al. 2001).

The collapse of the Grey Parrot population in Ghana sends a strong signal of what will happen to other populations if current levels of exploitation are allowed to continue. For years it appeared that the Ghanaian population was able to withstand the levels of exploitation that were exerted upon it, and although bans were intermittently placed on exports no serious efforts were made to control the trade. Retrospectively it must now be concluded that all through those years of exploitation the numbers of the species were growing smaller. In other words the trade was obviously not sustainable, and by extension other populations elsewhere in Africa, although seemingly healthy, are almost certainly in significant long-term decline. Immediate action is therefore needed to save the species. If the current trend of exploitation continues, countries with remaining healthy Grey Parrot populations (e.g. parts of Cameroon and DRC) are bound in the mid-term future to experience the catastrophic collapse that characterises the situation of the species in Ghana today, and that of the Timneh Parrot in most of its range.

6.4 Management of the parrot trade: bans and regulation

Two major approaches to managing the wildlife trade involve the regulation of trade through capture quota systems and the enforcement of trade bans (Pires and Moreto 2011). The goal is to minimise extraction from the wild in order to ensure sustainability and particularly to conserve threatened species. Ghana is a signatory to many international conservation treaties including CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora), and has national wildlife laws aimed at safeguarding biodiversity (Anon. 2013). The trade in Grey Parrots has undergone several embargoes over the years (Dändliker 1992). However, the lack of enforcement and corruption have rendered these laws virtually unobserved and toothless (Dändliker 1992, Smith and Walpole 2005). Outright trade bans have usually had mixed results: they can cause price hikes in some animals/animal products when demand remains high e.g. rhino horn *Ceratotherium simum*/*Diceros bicornis* and pangolins *Phataginus spp*./ *Smutsia spp*., and subsequently results in population declines (e.g. Pires and Moreto 2011, Biggs et al. 2013). In other species, trade bans have curtailed illegal capture (Pires and Moreto 2011). The quota system, on the other hand, also has its limitations. In developing countries like Ghana, where governance processes are not well developed and the lack of transparency and accountability is pronounced, quotas tend to be exceeded by large margins. In Mexico, where there was poor enforcement of a quota scheme, several tens of thousands of parrots were being poached illegally for the pet trade (Cantu et al. 2007). Trade regulation is a particularly challenging task for conservationists because of the enormity of the problem, as witness the geographical scales and numbers of species involved, the associated livelihood and socio-economic issues and the very low levels of priority and therefore funding given it by governments.

For example, overfishing in the open seas is difficult to control, as the resources to police fishing waters are simply inadequate (Pires and Moreto 2011).

6.5 Forestry management in Ghana: recommendations for the conservation of parrots and other frugivores

Forest loss in Ghana has become an important subject for discussion in recent times owing to diminishing cover attributable to forest fires, logging, agricultural expansion, mining activities, and other development projects (Hansen and Treue 2008, Appiah et al. 2009). About a third of Ghana's land area was covered by tropical high forest at the beginning of the 20th Century (Wagner and Cobbinah 1993). However, the high rate of deforestation meant that the country had lost nearly 80% of its forest cover towards the end of the century (Repetto 1988, Hawthorne 1989). The loss of forest is directly linked to biodiversity loss, and mitigation measures are urgently needed to protect Ghana's biodiversity, including parrots.

Various recommendations have been made in previous studies addressing the need for proper management of Ghana's forest habitats in order to safeguard wildlife and biodiversity in general (Arcilla et al. 2015). Holbech (2009), for example, proposed the nurturing of diverse agro-ecosystems to serve as zones of connectivity between small isolated forest blocks that at present are surrounded by monocultures. Such an intervention may prove useful for the survival of many wide-ranging species like hornbills that need to track food sources over long distances (Strong and Johnson 2001, Evans et al. 2005). Satellite communities of forest reserves may also be encouraged to undertake additional/alternative livelihood projects like fish farming, snail farming, apiculture and vegetable growing to subsidise family incomes from major crops during lean seasons and poor harvests (Appiah et al. 2009). Such measures could minimise people's overdependence on forests for farming (through shifting cultivation) and collection of non-timber forest products (Appiah et al. 2009). Historically, Ghana's forest reserves were set aside for the purposes of environmental protection and timber production (Hansen et al. 2012). The management of forest reserves has therefore heavily focused on the production aspect, to the detriment of both wildlife and the forest itself. For example, the practice of 'salvage logging' in the 1970s and 1980s, which permitted the unlimited felling of large trees as a means of 'cleansing' forests of over-mature timber, was clearly not detrimental to Ghana's Grey Parrots and other wildlife alone but also to the long-term diversity and functioning of the forest. This is because, apart from the provision of microhabitats and food resources for various organisms (including epiphytes), such trees could serve as 'stocks' of reproductive material for forest regeneration (Hawthorne and Abu-Juam 1995). An adequate number of very old mature trees in compartments earmarked for logging must be spared, as they are essential for hole nesting species such as parrots, hornbills and arboreal mammal species (e.g. Marsden and Jones 1997, Schmid 1998, Monterrubio-Rico and Enkerlin-Hoeflich 2003, Aitkin and Martin 2007). Finally, Ghana should implement the reintroduction of shade cocoa *Theobroma cacao* agriculture, which is compatible with maintaining large trees on farmland. Such a policy should be implemented in conjunction with an overhaul of the current forestry policy which disenfranchises farmers from ownership of trees on farmlands (see Sargent et al. 1994, Ruff 2011). This approach to cocoa agriculture is congruent with the land sharing principle (e.g. Phalan et al. 2011, Hulme et al. 2013).

6.6 Future research priorities

The charismatic personality of the Grey Parrot, considered a better 'talker' than any other parrot species, makes it one of the most popular of pets (Collar 1997). However, other characteristics of the species—tendency to be quiet and cryptic when feeding, the formation of large social aggregations that make them unevenly distributed, and the common habit of performing long-distance flights between feeding and roosting sites—make it extremely difficult to study in the wild (Marsden et al. 2015). Knowledge of the species in the wild is therefore limited, and many sources of information are anecdotal (Martin et al. 2014). However, increasing concerns about dwindling populations and sustainability of trade in the species has stimulated some research, including this study and a similar one on the island of Príncipe (Valle 2015). The findings of my study indicate a clear and present danger to the survival of the species in Ghana whereas thriving populations were found in Príncipe. In spite of these modest attempts to improve knowledge about the Grey Parrot, much more research needs to be conducted.

First, more precise population trends for the *Psittacus* species are now urgently needed in order to assign them a more realistic conservation status. Repeat surveys in countries such as Guinea Bissau, Nigeria, Cameroon, Gabon and DRC are highly recommended. These countries have baseline data from previous surveys conducted in the last two decades (see Dändliker 1992, Fotso 1998a, 1998b, McGowan 2001, Clemmons 2003). In Ghana, where this study has already achieved this objective, there is a need for focused research on the biggest population identified in the southwest of the country near Cape Three Points Forest Reserve. Further studies on this population should endeavour to determine population size, examine demographic characteristics, study feeding and reproductive ecology, and habitat use where possible. Other priority areas for further research and conservation of the Grey Parrot are the twin protected areas of Nini Suhien National Park and Ankasa Resources Reserve, Kakum National Park and Assin Attandanso Resource Reserve, as well as the Subri River Forest Reserve.

Second, the study of movement and spatial ecology of the species should investigate the potential use of GPS tracking devices (see Herrod et al. 2013, Kennedy et al. 2015). This area of study has the potential to generate a great deal of information to improve our knowledge of the ecology of the *Psittacus* parrots. The array of information may include knowledge on essential habitats and foraging pathways, as well as elucidation of parrot responses to human perturbation of natural ecosystems (Kennedy et al. 2015). These proposed studies are directly applicable to frugivores in general, and especially hornbills, which have similar breeding requirements to parrots.

Third, the study of parrots in Ghana should be extended spatially to include regions of higher latitude in the country. Particularly, the Senegal Parrot *Poicephalus senegalus* requires immediate attention as it is currently heavily traded (BirdLife International 2015). The global population of the Senegal Parrot has not been quantified, and even though it is not thought to be in decline (Collar 1997), much of the information about the species is based on anecdotal evidence (Martin et al. 2014). It is therefore imperative to conduct baseline studies to produce an estimate against which future monitoring can be compared before the species suffers a similar fate to the Grey Parrot.

Fourth, there is the need for research into trends and patterns of trade in other range states by means of questionnaires, as well as assessments of the performance of national and international laws and the agencies that are supposed to enforce them. This much needed information on the effectiveness of trade management for the Grey Parrot could be generated by the use of questionnaires, which is a method that has proved useful in gathering such data in relatively short periods. For example, Martin et al. (2014) used questionnaire to gather information on the status of the larger parrots of Africa and Madagascar in a cost-effective manner and a relatively short period.

Finally, the study of urban Grey Parrot populations could be no less informative than studies of forest-based birds, because their ecology in urban environments may hold essential cues to their successful management wherever they breed. Their feeding habits and resource-tracking patterns, reproductive ecology, population trends, as well as impact on other urban species could be insightful.

6.7 References

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