POPULATION VIABILITY AND CONSERVATION OF GREY PARROTS PSITTACUS ERITHACUS ON THE ISLAND OF PRÍNCIPE, GULF OF GUINEA

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POPULATION VIABILITY AND CONSERVATION OF GREY PARROTS PSITTACUS ERITHACUS ON THE ISLAND OF PRÍNCIPE, GULF OF GUINEA

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Abstract

Parrots are among the most endangered birds in the world, owing to the international pet trade, and habitat degradation. Grey Parrot *Psittacus erithacus*, the most traded wild-caught species, has suffered a steep decline across its vast African range. This PhD investigates Grey Parrot's ecology to understand the mechanisms by which harvest and habitat loss affect populations. The island of Príncipe was chosen as a study area owing to its healthy Grey Parrot population, its tradition of parrot harvest and the disturbed-to-pristine range of habitats. Parrot densities were exceptionally high (mean±SE: 53±3 parrots km^{-1}), and their distribution within the island was shown to change significantly between pre- and post-breeding season. The presence of nest tree species was the best predictor of densities in the former (F=2.99, p=0.07), while slope and food tree species were in the latter (F=3.0, p<0.05 and F=8.04, p<0.01). Variation in habitat use across seasons highlights the importance of opportunely timed surveys, and the need of preserving a matrix of habitats. Three simple and inexpensive methods were tested, which may be useful where more precise methods cannot be used. Simple encounter rates were shown to be a workable proxy for actual densities: a relationship was found between the two (R^2=0.8, df=9, p=0.01). Long watches proved to be far less accurate and suitable only in limited cases (i.e. enough vantage points overlooking small areas and numerous encounters). Counts along flyways were suggested to be a good monitoring method, although further testing is required. Nest densities were found to be very high (mean±SE: 16.8±7.9 and 72.4±26.2 nests km^{-2} in secondary and primary forest respectively) compared to those elsewhere. The habitat characteristics measured didn't affect productivity, suggesting that cavity characteristics may be more important. The best demographic data available on the species, were used to build a Population Viability Model to investigate its population dynamics in the face of harvest and habitat loss. In Príncipe, Grey Parrots were shown to have increased rapidly after a trade ban was put in place, highlighting the recovery potential of the species. Harvest alone was shown to be harmless only when small quotas (e.g. 600 chicks year^{-1}) are yielded from large populations, while habitat loss lowered the predicted maximum population size. The interaction of these threats can be much more unpredictable. The effects of harvest are worsened if poorly regulated or techniques that include the harvesting of adults are used. Extinctions were predicted to occur with significant delay (≥40 years), and the conservation implications were discussed. Finally, the contribution of this thesis to the understanding of Grey Parrots ecology and conservation is highlighted and research priorities identified.

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Chapter 1. Population Viability and the Conservation of Parrots: an introduction

1.1. The parrot conservation crisis

The causes of the present rapid decline of global biodiversity are predominantly anthropogenic, with extinction rates a thousand times higher than ever recorded in the fossil record (Millennium Ecosystem Assessment 2005). This global species loss has been effectively regarded as the earth's sixth mass extinction (Berkunsky et al. 2012). Among the primary and most immediate drivers of such severe loss of biodiversity are the destruction or degradation of habitat (Noss et al. 1994), climate change (Thomas et al. 2004), invasive species (Gurevitch and Padilla 2004) and overexploitation (Pauly et al. 1998, Milner-Gulland and Bennett 2003). The mutual interaction between two or more of these factors may make their effects on native species more severe and difficult to diagnose (Didham et al. 2007).

Some species are more vulnerable than others to the risk of extinction, depending on their biological attributes and habitat/niche (Purvis et al. 2000). Since the resources available to conservation practitioners are always limited, over the years their effort has greatly benefited from being prioritised according to an evaluation of each taxon's extinction risk (Lamoreux et al. 2003). Psittaciformes are among the most endangered bird orders in the world (Collar and Juniper 1992). Of the 356 living species, 105 (29.5%) are threatened and 16 (4.5%) are currently considered Critically Endangered (IUCN 2014). Owing to their ability to talk, their colours and their capacity to form close bonds with their keepers, they are charismatic birds and make ideal flagship species for the conservation of a number of tropical ecosystems (Snyder et al. 2000). Parrots play a crucial role in the functioning of the ecosystems they inhabit as seed

dispersers (Southerton et al. 2004), or pollinators (Vicentini and Fischer 1999, Hingston et al. 2004), although these aspects are yet poorly known.

Despite their critical conservation status and their popularity among the general public, parrots are a largely understudied taxon for a number of reasons: they are long-lived, wide ranging, unpredictable, non-territorial and highly cryptic when perched (Collar 1998). Owing to the relative inaccessibility of their nests and their long life cycle, quantifying specific life traits is often problematic (Beissinger 2001). Because of this, the population size, habitat requirements and conservation status of many parrot species is not at all known (Collar 1998). The continuous degradation or loss of their habitat worldwide is regarded as the main cause of worldwide population declines in parrots (Snyder et al. 2000). While ecological flexibility has allowed some parrot species to adapt well to habitat changes (Marsden 1998, Bonadie and Bacon 2000, Vaughan et al. 2006), others are particularly vulnerable to environmental change owing to their highly specialized niches (Roth 1984, Matuzak et al. 2008). The popularity of parrots among the general public constitutes one of the main threats to this taxon, as they are commonly and widely harvested from the wild to be sold on the pet trade market (Collar and Juniper 1992). Juniper and Parr (2003) estimated that habitat loss alone affects 73 of the species currently endangered, that trapping for the pet trade alone affects 39 species, and that 28 species experience both forms of pressure.

Approaches to parrot conservation have been varied and often tailored to each case. Besides the more obvious strategies focusing on the preservation of their habitat and ending or mitigation of known threats, some unique species-specific approaches have been developed. Programmes for the conservation of Lesser Antillean parrots have hinged on education and national pride (Butler 1992). Ecotourism has been used as a base for the conservation of macaw species in Peru, Bolivia and Brazil (Munn 1992). Artificial nest boxes have been installed to enhance macaw populations in Peru (Nycander et al. 1995, Vaughan et al. 2005). Sustainable harvest schemes have been proposed for some neotropical species (Beissinger and Bucher 1992a). In the case of extremely small populations, state-of-the-art of intensive management techniques have been

employed, e. g. the relocation of flightless Kakapos *Strigops habroptilus* to predator free islands *(Clout and Merton 1998)*; the captive breeding, cross-fostering, double clutch inducing and supplementary feeding of the endangered Echo Parakeets *Psittacula eques* (Jones and Merton 2012), and the first captive reproduction through artificial insemination of the Critically Endangered (and possibly extinct in the wild) Spix's Macaw *Cyanopsitta spixii* (Hammer and Watson 2012).

1.1.1. Habitat loss and fragmentation

Twenty four percent of earths' terrestrial surface has been converted to agricultural land and, if we exclude a further 30 % of deserts, the remaining undisturbed habitats, are heavily fragmented (Millennium Ecosystem Assessment 2005). These remaining areas pose an insurmountable barrier to the dispersal of many species, increasing the proportion of edge habitat and its detrimental effects, and increasing the probability of invasion by generalist and alien species (Noss et al. 1994). The negative influence of fragmentations has been shown to drive the extinction of animal populations even within managed and protected areas (Woodroffe and Ginsberg 1998).

The general morphology of parrots suggests that they have evolved in forests, and the vast majority of species are still tied to tropical and subtropical forested biomes (Collar 1997). All parrots feed mainly on seeds, fruit, nectar, pollen and buds (Forshaw 1989). Humid tropical forests host the highest parrot diversity and they are suffering a constant decline in their extent and quality (Snyder et al. 2000). It is estimated that between 1990 and 1997, 5.8 ± 1.4 million ha of the world's humid tropical forest were lost each year and an additional 2.3 ± 0.7 million ha were visibly degraded (Achard et al. 2002). Although at a reduced rate, deforestation continued in recent years with a further 27.2 ± 2.28 million ha lost globally between 2000 and 2005 (Hansen et al. 2008). Proximate causes of tropical deforestation are agricultural expansion, wood extraction and infrastructure extension, while the underlying factors are economic (economic growth, change or development, commercialisation), institutional (change of

political economy), technological (technological change or progress), cultural (or socio-political) and, ultimately, demographic (human population dynamics) (Geist and Lambin 2001).

Deforestation can have different effects on parrot populations, and the mutual interactions of these may exacerbate their severity (Didham et al. 2007). Changes in food resource availability and accessibility have been linked to the decline of wild populations (Saunders 1990, Berg et al. 2007). The majority of parrot species nest in natural tree cavities, to which they may make only minor adaptations, so that the number of suitably sized trees limits breeding densities (Beissinger and Bucher 1992b, Munn 1992). Other specific habitat requirements may include access to suitable roosting sites (Snyder et al. 2000), and water and minerals i.e. salt licks (Lee et al. 2010). Human populations often tend to concentrate in areas rich in biodiversity (Balmford et al. 2001), thus the fragmentation of tropical forests is caused and rapidly followed by the establishment of human settlements and an increase in direct exploitation (Wilkie et al. 2000). Moreover, the vicinity of agricultural land encourages crop raiding by a number of parrot species (Bucher 1992). For many bird species, fragmentation is known to disrupt metapopulation dynamics, where the persistence of wild populations relies on a complex of interdependent subpopulations affected by recurrent extinctions and linked by recolonization from one or more large reservoir populations (Hanski 1998). This is likely to be the case for parrots as well, although the importance of metapopulations in Psittaciformes is poorly understood (Wilson et al. 1994). Finally, as a secondary effect, the isolation of small populations has been known to be responsible for the extinction of parrot species through inbreeding depression and increased vulnerability to natural catastrophes (Gilpin 1996, Juniper 2002).

Although the preservation of parrots' preferred habitat (i.e. tropical and subtropical forests) is paramount for the conservation of many species (Snyder et al. 2000), a growing body of evidence suggests that over the annual cycle some parrots require a variety of habitats and forest types to sustain healthy populations (Galetti 1997, Renton 2002, Matuzak et al. 2008). It is difficult to estimate the extent to which habitat loss is a threat to parrots compared to

trade, but it is often the case that the former exposes them to higher risk of the latter, and combined they pose a major threat (Collar and Juniper 1992).

1.1.2. International pet trade

The international wildlife trade is estimated to involve billions of live animals and animal products worldwide each year, threatening about one-third of all bird and mammal species (UNEP-WCMC 2014). Around a thousand timber species are threatened with extinction due to felling (Oldfield et al. 1998), and 75% of fisheries are fully or overexploited (Hilborn et al. 2003). Legal wildlife trade alone has been estimated to be worth more than USD 8 billion a year globally (Zhang et al. 2008). Nonetheless, real figures are much higher since illegal trade is estimated to be a major criminal enterprise, surpassed only by the illegal drug trade and human trafficking, with an annual revenue of further USD 8-10 billion (Pires 2012).

Parrot trade makes up a multi-million dollar share of this market. In response to a growing demand, the number of neotropical parrots traded annually went from fewer than 100,000 in the 1970s to more than 250,000 in the 1980s (Thomsen et al. 1992). In Africa, from 1982 to 2001, the number of wild-caught parrots which entered international trade reached over 657,000 individuals of just one species (Grey Parrot *Psittacus erithacus,* although a small minority were the now-split Timneh Parrot *Psittacus timneh*) (UNEP-WCMC 2014). The multi-million dollar parrot trade usually has three potential markets: international, local, and extended local (Weston and Memon 2009). The international market is where parrots are exported (legally or illegally) from country of origin to another country, and is usually regulated by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 2015). Until 1992, the US represented one of the biggest importers, with 80% of the international market for neotropical psittacines (Munn 2006). In 1992, the Wild Bird Conservation Act banned the importation of parrots into the US and significantly diminished demand in the international trade, and in 2007 the European Union passed a similar act. Data suggest that the ban put in place by

the US may have had a beneficial impact on nest poaching (Wright et al. 2001, Pain et al. 2006), but the overall effects are difficult to evaluate. Parrot trade may have shifted to local and extended local markets, which represent the bulk of the parrot trade in Latin America (Gonzalez 2003). The local markets are where parrots are taken from their habitats and either kept by the family who caught them, or sold in nearby villages, and although little money is gained for a single transaction, a large number of parrots may be a reasonable supplement to a family's income (Thomsen and Mulliken 1992). Finally, in some regions (e.g. Peru), the local market is extended further as the wild-caught parrot are transported and traded hundreds of kilometres away from the trapping region with several chains of people making a living from the trade (Weston and Memon 2009).

Data suggest that there may be a great potential in developing management programmes for the sustainable harvest of commercially valuable species, but the lack of good biological and demographic information on almost all parrots, seriously hinders efforts to implement such schemes (Beissinger 2001).

1.1.3. Other threats

There are a number of other factors which are known to threaten some parrot species. The colourful feathers of some species are highly valued as tribal ornaments in some regions (McCormack and Künzlè 1996, Mack and Wright 1998) and as traditional medicinal remedies (Adjakpa et al. 2002). The hunting of parrot species for food is not common, but not unknown (Martuscelli 1995, Melo 1998). Introduced species have been known to pose a major threat to island species in the form of competition for food and nest sites (Wilson et al. 1998), and predation (Kuehler et al. 1997). Though not well documented, it is also reasonably likely that introduced diseases or abnormal surges in the natural incidence of parasitism may have an impact at a species level (Snyder et al. 1987). Sometimes more common parrots may act as a reservoir for infection for more endangered species as it is suggested to be the case of the beak and feather disease virus threatening the last wild population of the

critically endangered Orange-bellied Parrot *Neophema chrysogaster* (Peters et al. 2014). Natural disasters have been shown to threaten parrot species with a limited distribution range, as they may critically reduce the availability of suitable breeding sites (Christian et al. 1996). Finally, most of the causes of parrot decline may be exacerbated by rapid global climate change (Harris et al. 2012).

1.2. Parrot populations: density, demography and dynamics

1.2.1. Estimating parrot abundance

Parrots are a highly threatened taxon but quantifying their degree of threat may be challenging. Measures of abundance and range size are the base of any evaluation of extinction risk and, in turn, of the prioritisation of conservation effort (Mace et al. 2008). Despite parrots' endangered status, little is known about the size of their populations in the wild, and density estimates are available only for 25% of the world species, regardless of their conservation status or biogeographical region (Marsden and Royle 2015). Estimating parrot populations presents several challenges (Casagrande and Beissinger 1997). In some contexts parrots may fly long distances between nesting, roosting, and feeding areas in large flocks composed of several species (Chapman et al. 1989). They often inhabit dense forests, where visibility is poor, and their cryptic coloration and secretive behaviour inhibit detection when they perch (Collar 1998). Finally, capturing and marking parrots is difficult, so that mark-resighting methods are rarely used (Casagrande and Beissinger 1997). Parrot populations are usually estimated using one of the following three methods: roost counts, mark-resighting and distance sampling.

Roost count surveys involve counting all the birds leaving or arriving at roosts (Bibby et al. 1992), but this method is based on the rarely tested assumption that all roosts are found and surveyed (Casagrande and Beissinger 1997). Although possibly suitable for island populations or small study areas (e.g. Snyder et al. 1987) several factors may significantly affect the accuracy of the

method, notably inconsistency in use of roosts e.g. the daily and seasonal variation in roost attendance (Saunders 1979, Kalina 1988), visibility (Cougill and Marsden 2004), and weather conditions (Wilson and Anderson 1985).

Mark-resighting methods involve catching a number of individuals, marking them individually and releasing them back into the wild, with the assumption that they will randomly mix with the original population (Bibby et al. 1992). Population size is then estimated after a second sample is subsequently re-sighted, as it is assumed that the number of marked individuals then have the same ratio to the total numbers as the initial number of marked individuals has to the total population (Cormack 1968). Nevertheless, capturing parrots is very difficult as they are intelligent, observant and sociable canopy-dwelling birds (Meyers and Pardieck 1993, Meyers 1994a). Once parrots have been caught, a further challenge is to find means of individually marking them that would be durable enough and yet not affect their survival. Split metal rings are the cause of injuries, possibly affect survival of marked birds, and mean that that the bird must be recaptured (Meyers 1994b). Colour rings have been successfully employed on some species (Meyers 1995, Phillips and Dudík 2008), but parrots have relatively short tarsi and the rings are hard to re-sight in high canopy or closed forest habitats. Patagial tags have been used to study cockatoos (Rowley and Saunders 1980), but once again they have been found to affect the marked birds' survival (Saunders 1988). Neck collars have been successfully employed on small billed parakeets (i.e. Monk Parakeet *Myiopsitta monachus*) (Senar et al. 2012), nonetheless effects on birds behaviour are yet to be tested.

Distance sampling is the most accurate population estimate methods currently available to parrot ecologists (Marsden and Royle 2015). It encompasses a set of methods in which distances from a line transect or point to detected birds are recorded, from which, in turn, the detectability and density of parrots are estimated (Thomas et al. 2010). Line transects provide more sightings and tend to have lower bias and higher precision, but, where navigation is difficult, point counts are to be preferred (Buckland et al. 2008). Distance sampling also gives

researchers the opportunity to take into account those factors which may affect detectability (e.g. habitat, time of day, weather conditions, observer, bird behaviour) through the inclusion of one or more covariates (i.e. multiple-covariate distance sampling) (Marques and Buckland 2003, Marques et al. 2007). Casagrande & Beissinger (1997) have compared the use of roost counts, mark-resighting and distance sampling to estimate a population of Green-rumped Parrotlets *Forpus passerinus* and found that the last method was the most accurate, precise and effort-effective, with a clear advantage of line transects over point counts.

Distance sampling is the preferred method for population estimates by bird ecologists (Newson et al. 2008), and more than half of all parrot population estimates have been generated with this method (Marsden and Royle 2015). However, distance sampling is time-consuming and resource-demanding, and requires a minimum number of encounters (i.e. 80 or more) to allow a reliable density estimation (Buckland et al. 2008). In a world where economic resources are always limited, and surveying skills patchily available, there has been a great interest in testing new practical, rapid and inexpensive methods to provide usable metrics of animal abundance (Lancia et al. 1994, Carbone et al. 2001).

1.2.2. Demography and population dynamics

Estimating the size of a population is only a first step in the true assessment of a species conservation status. To understand the way that that population may grow or go extinct ecologists need to look at the way it is regulated (Newton 1998). The dynamics of a population is the variation of its size and structure over time. These are the result of losses and gains of individuals due to four key demographic processes: recruitment, survival, emigration and immigration (Sibly and Hone 2002). Population dynamics depend on demographic rates, and understanding how a change in the latter is translated into a change of population growth is therefore the key to identifying the causes of population declines, and, ultimately, to guide management decisions to halt or reverse extinctions (Caughley 1994). These dynamics may also change in large

populations, as some demographic parameters can be density-dependent e.g. Allee effects (Boyce 1992, Stephens et al. 1999). In extremely small or island populations inbreeding and lack of breeding opportunities become more likely due to geographic isolation (Gascoigne et al. 2009).

Differences in life-history traits are ultimately responsible for species' vulnerability to different threats and, thus, a better understanding of those differences may be crucial to the conservation and management of parrots (Beissinger 2001). It is known that birds may live up to three times longer than mammals of equivalent body mass (Austad 1993), and that the order Psittaciformes includes species with exceptionally long lifespans for their size (Holmes et al. 2001). The oldest parrot ever recorded in captivity was apparently a 92 years old Salmon-crested Cockatoo *Cacatua moluccensis* (Young et al. 2012). Evolutionary theories of ageing suggest that the intrinsic lifespan of a species should increase as the rate of extrinsic mortality (e.g. from predation or disease) decreases (Austad and Fischer 1991). It is also known that parrots typically have small clutch sizes and few broods per year (Forshaw 1989), that they nest in tree cavities, the availability of which may limit the yearly breeding output (Beissinger 2001). Moreover, medium- and large-sized species may not reach age of first breeding until two to five years of age (Young et al. 2012). Nonetheless, empirical estimates of lifespan, breeding output, survival and age of first breeding in the wild are either missing entirely or highly imprecise for most parrot species (Sandercock et al. 2000). This is because ageing adult parrots and marking them individually poses many challenges (see § 1.2.1), and the average duration of studies is generally too short in comparison to lifespans (Young et al. 2012).

1.3. Population Viability Analysis as a tool for parrot conservation and management

Population Viability Analyses (hereafter PVAs) are stochastic simulation models that use demographic data from a population to make quantitative predictions about its size and the likelihood of extinction over time (Beissinger and

McCullough 2002). PVAs are closely related to the concept of Minimum Viable Population (MVP), where the models are used to estimate the smallest population size with a 95% chance of remaining extant over a 100-year period (Shaffer and Samson 1985). The prospect of quantifying an MVP has been of great interest to conservation practitioners, but the concept has since been challenged both on theoretical and empirical grounds (Flather et al. 2011). PVAs were first developed in the 1980s as a method for evaluating the extinction risk of those species which had been reduced to very small and isolated populations (Gilpin 1996). In recent years, however, models have developed significantly and have become a relatively common tool for the study and management of threatened and invasive species alike (Beissinger and Westphal 1998, Pruett-Jones et al. 2007). Increasing computing power has allowed conservation scientists to create ever more complex models which may incorporate molecular genetics, metapopulation dynamics and geographical information, although this also increases the amounts and types of data needed (Beissinger 2002).

Despite their widespread use, PVA models are often difficult to develop owing to a lack of life-history data, and imprecise models may, of course, produce inaccurate and misleading results (Reed et al. 2002). Models should ideally be built to reflect as closely as possible the essential features of the ecology of the organism, and their accuracy and precision is proportional to the accuracy and precision of the demographic information included (Boyce 1992). The outcomes predicted by PVA models are often uncertain owing to poor data, difficulties in the estimation of the life-history parameters, inability to validate models in the field, and complications in evaluating the effects of alternative model structures (Beissinger 2002). Several authors have warned against using absolute extinction risks resulting from PVA simulations, and suggest instead that outcomes should be considered proportionately to limitations of the data (Beissinger and Westphal 1998). Thus, the focus has moved to sensitivity analyses, where an array of possible scenarios is theorised through the methodical variation of key parameters in the model, and their probability of occurrence evaluated (e.g. Heinsohn et al. 2015).

The development of PVAs has been entwined with the study of parrot ecology since its conception (Gilpin 1996). In the case of parrots, the development of population models has often been aimed at quantifying the effects of the harvest for the pet trade, and at exploring the possibility of managing wild populations to implement some form of sustainable harvest (Beissinger and Bucher 1992b, a). Since most parrots are impossible to age once they reach adulthood, the development of stage-based models (i.e. models based on the species' life stages, rather than on a sequence of successive years) a has improved the accuracy of the models applied to parrot species (Caswell 1989). To date, PVAs have been used to plan the management of the invasive Monk Parakeet *Myiopsitta monachus* (Pruett-Jones et al. 2007), for the evaluation of the extinction risk of endangered species like the Black-billed parrot *Amazona agilis* and Palm Cockatoo *Probosciger aterrimus* (Koenig 2008, Heinsohn et al. 2009), to evaluate the effects of introduced predators on Swift Parrots *Lathamus discolor* (Heinsohn et al. 2015), and to inform the management of Orange-bellied Parrots *Neophema chrysogaster* (Drechsler et al. 1998).

1.4. The Grey Parrot in Príncipe: a case study

The Grey Parrot *Psittacus erithacus* is endemic to the humid tropical forests of Central-Western Africa (Juniper and Parr 2003), and has recently been uplisted to 'Vulnerable' after a rapid decline was suspected in wild populations across its vast distribution range in the last 20 years (BirdLife International 2014b). As for many other parrot species, harvest for international trade and on-going habitat deterioration have been identified as the main causes of such a dramatic decline (Snyder et al. 2000). The Grey Parrot is one of the most popular avian pets owing to its mimicry ability, and it is the object of a multimillion-dollar business which takes tens of thousands of individuals from the wild each year (CITES 2006). At the same time, its habitat is rapidly disappearing, with an estimated loss of 0.85 ± 0.3 million ha per year in the 1990s in central and west Africa, and an even further expansion of industrial logging since the Millennium (Achard et al. 2002, Laporte et al. 2007). Despite the charisma of the species

and its rapid decline, little is known about its specific habitat requirements and conservation status, as most research has focused on the extraordinary cognitive capabilities of the species (Pepperberg 2008).

Príncipe, in the Democratic Republic of São Tomé and Príncipe, is a small island (139 km^2) that is home to a large and isolated population of Grey Parrots (Jones and Tye 2006, Melo and O'Ryan 2007). The human population of the island has a long tradition of parrot harvesting for the international pet trade, extracting an average of 600 birds per year from the wild in the 1990s (Juste 1996, Melo 1998, Fahlman 2002). In 2006, a regional ban on all trade was put in place although some harvest is still carried out illegally for the local market (pers. obs.). All accessible areas of the island (i.e. the northern half) have been cleared and planted with cocoa *Theobroma cacao*, coffee *Coffea spp.* and coconut *Cocos nucifera* plantations, while most of the southern half has been left untouched and is covered by original lowland rainforest (Exell 1973). Today, most of the farms have been abandoned and overgrown by secondary forest, and the north of the island holds a wide range of more or less regenerating tropical forest habitats (Jones and Tye 2006).

Owing to its small size, variety of forest habitats, history of intensive trade and relatively healthy but closed Grey Parrot population, Príncipe offers a unique opportunity to study the basic ecology and population dynamics of this species as well as the effects of the pet trade and habitat degradation on its population.

1.5. Study species: the Grey Parrot

1.5.1. Taxonomy

The African Grey Parrot has been long considered one species, unique to its genus, with two distinctive and allopatric races: *Psittacus erithacus erithacus* and *Psittacus erithacus timneh*. These have been recently split into two distinct species on the basis of morphological evidence (Fig.1.1), and apparent (at least

former) parapatry: the Grey Parrot *P. erithacus* ranging from east of the Bandama River in Ivory Coast to Kenya, and the Timneh Parrot *Psittacus timneh* ranging from west of the Bandama River to Guinea-Bissau (del Hoyo and Collar 2014). Grey Parrots from Príncipe and Bioko were at one stage, on the basis of morphological differences, proposed as a separate species (i.e. *P. princeps*) (Alexander 1909). Bannerman (1914) reclassified them as a subspecies (i.e *P. e. princeps*) and later Amadon (1953) considered them part of the nominate race. Recently the re-instatement of subspecific status for Príncipe birds has been proposed on the basis of further genetic evidence (Melo and O'Ryan 2007).

Figure 1.1. Left, Grey Parrot *Psittacus erithacus* (photo: Keith Allison) and Right, Timneh Parrot *Psittacus timneh* (photo: Snowmanradio).

1.5.2. Distribution

The range of the Grey Parrot stretches across the lowland moist forest of West and Central Africa, from south-eastern Cote d'Ivoire and Ghana, eastwards through Nigeria, Cameroon, Gabon, the Republic of Congo, northern Angola and the Democratic Republic of Congo (DRC; Fig. 1.2; Juniper and Parr 2003). They are absent from Benin (Dändliker 1992b, Dowsett and Dowsett-Lemaire 2011) and Togo, with the exception of a feral population in Cotonou (Martin et

al. 2014). The eastern margin of the range extends just over the Albertine Rift into Uganda (Carswell 2005, Twanza and Pomeroy 2011), western Kenya (Lewis and Pomeroy 1989), and north-west Tanzania (Dowsett and Forbes-Watson 1993). The species is present on the islands of Príncipe (São Tomé and Príncipe) and Bioko (Equatorial Guinea). A small population of most probably feral origin is also known to exist on São Tomé Island, although its size and status are yet to be quantified (Melo 1998; R. Lima *in litt.* 2013). Other feral populations of several hundred each are noted in Kampala, Uganda, and Kinshasa, DRC (Martin et al. 2014).
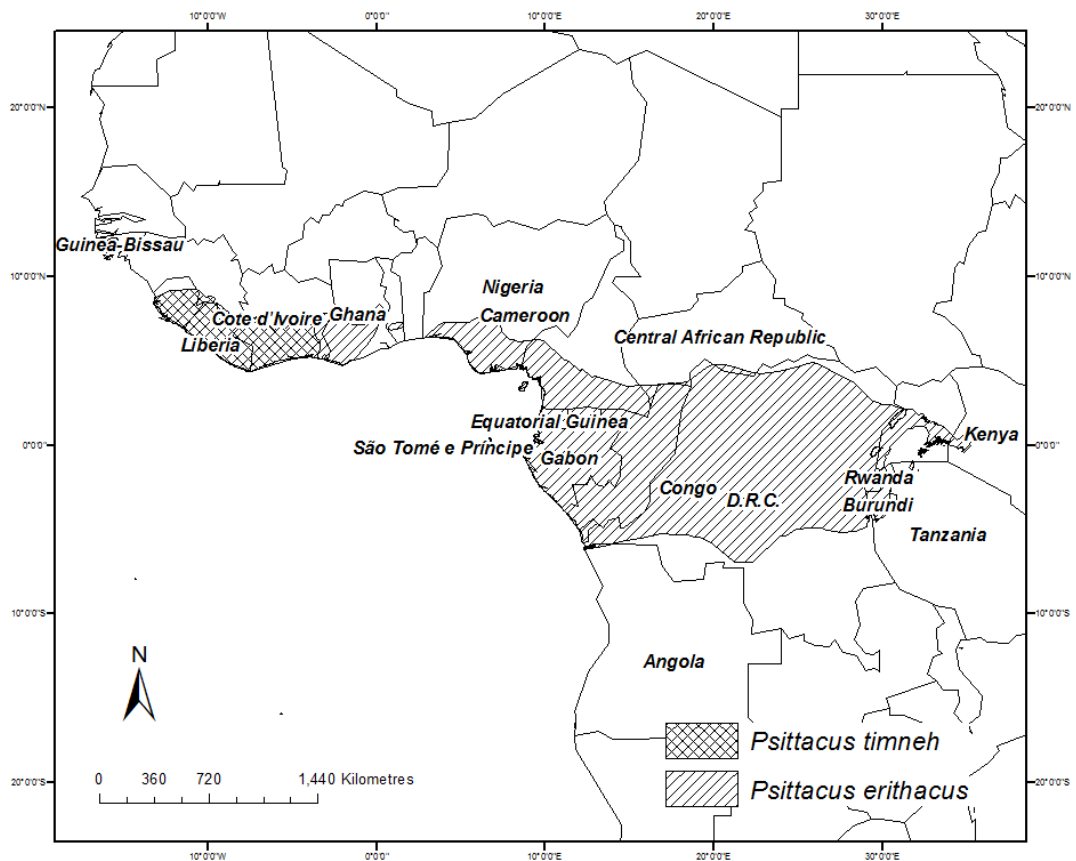
Figure 1.2. Distribution range of the two *Psittacus* species: Grey Parrot and Timneh Parrot.

1.5.3. Status and population trends

Once widespread across West and Central Africa, Grey Parrots have seen a rapid decline across the whole distribution range, owing to harvest for the parrot trade and habitat loss (BirdLife International 2014b).

In Ghana, serious population declines had been reported since the late 1980s (Grimes 1987). Surveys in the early 1990s failed to find the large flocks and or roosts that had been previously reported from the same areas (Dändliker 1992a). Today, the species has disappeared from, or is very rare in, most of its historical range, including protected areas (N. Annorbah et al. *submitted*). Recent information on population trends suggest that Grey Parrot populations in Côte d'Ivoire have undergone a similar fate (Marsden et al. 2013), most probably owing to the regular export to Guinea for re-export (Clemmons 2003). In Nigeria, the species was already highly fragmented in range in the early 2000s, having disappeared from large portions of the country (McGowan 2001). Although more recent systematic surveys are lacking, a dramatic decline has been observed nationwide, even within protected areas (e.g. Olmos and Turshak 2009). Declines have also been reported in Cameroon, where the species has now disappeared from many areas where it was very common only 30–50 years ago (Tamungang and Cheke 2012). Population estimates carried out in 2008–2011 were 30–60% lower than those made in 1996–1997 (Fotso 1998b), although comparison should be made with caution as methods were different. Nonetheless, Grey Parrots are still abundant in some Cameroon protected areas (i.e. Lobeke and Compo Ma'an National Parks), with densities greater than 50 birds km^{-2} (Marsden et al. 2013). The status of Grey Parrot populations in DRC is poorly known owing to the size and inaccessibility of the country. Fotso (1998a) made some estimates in the Equateur region based on roost counts, but these were not repeated, and no other surveys were carried out in the country. Anecdotal information reveals that the species, which was once common and widespread, after being heavily harvested for decades is now disappearing from western areas (e.g. Salonga National Park) (Hart 2013).

Consistent with this information, recent surveys in the Maniema and Orientale Provinces have found very low densities (i.e. 0.33 birds km^{-2}; (Marsden et al. 2013). Large declines have been recorded in the Republic of Congo since the early 2000s particularly in Bomassa, close to Lobéké, Ndoki and Nouabalé-Ndoki NPs, which may be linked to high levels of trapping along the Sangha river (Martin et al. 2014). Updated information on the species' status in Gabon, Central African Republic and north Angola is lacking (BirdLife International 2014b).

In East Africa, populations are declining or have disappeared altogether. In Uganda, surveys conducted in 2002–2003 reported populations as small and fragmented (Amuno et al. 2007). The species is now scarce or absent from areas where it was abundant just 60 years before (Jackson and Sclater 1938, Carswell 2005). In Kenya it is restricted to the Kakamega Forest (only 230 km^2) (Madindou and Mulwa. 2010), despite being previously widespread (Lewis and Pomeroy 1989). In Rwanda, Grey Parrots have declined sharply and are now restricted to few forest fragments (e.g. Nyungwe National Park), while in Tanzania only a very small population remains in the far north-west of the country (Martin et al. 2014).

1.5.4. Habitat and ecology

Grey Parrots have been observed in a variety of habitats, namely forest edges, clearings, gallery forest, mangroves, wooded savanna, cultivated areas, and even gardens; but they typically inhabit dense forest (Juniper and Parr 2003). The species is known to make seasonal movements in the driest parts of its range, but little is known about these (Benson et al. 1988). It is a highly gregarious species and typically forms large roosts that can host several thousand individuals (Dändliker 1992a). Grey Parrots feed on a variety of fruits and seeds (Tamungang and Ajayi 2003), with a marked preference for oil palm *Elaeis guineensis* fruits (Brosset and Erard 1986, Benson et al. 1988). Although it has been known to nest in rock cavities (Marsden et al. 2013) or even buildings (Twanza and Pomeroy 2011), the Grey Parrot can be considered an

obligate secondary tree-cavity nester, making it particularly vulnerable to the low availability of suitable cavities owing to tree-felling or competition (Forshaw 1989). The species establishes long-term pairs and lays one to four eggs once per year with a marked variation of the laying dates according to region, although it is probably mainly a dry-season breeder (Benson et al. 1988). Incubation and fledging both take around 30 days (Juniper and Parr 2003). In captivity, Grey Parrots demonstrate highly developed cognitive abilities (Pepperberg 2008) and extraordinary mimicry skills (Pepperberg 1981), peculiarities that make them extremely valuable on the international pet market. Nonetheless the use and occurrence of these skills in the wild is poorly known (Cruickshank et al. 1993, Gautier et al. 1993).

1.5.5. Threats and conservation

Habitat loss undoubtedly has had a significant impact on Grey Parrot populations, but this is difficult to quantify with any precision (BirdLife International 2014b). Data seem to suggest a positive relationship between the status of the species and the status of primary forest (Dändliker 1992a, Clemmons 2003), and densities are reported to be higher in better-preserved forests (Juste 1996, Marsden et al. 2013). Even where deforestation is not a major threat, the loss of keystone habitat resources, especially nest cavities and roost sites, may be a major problem (Tamungang & Cheke 2012, Annorbah in prep.).

Trapping for the international pet trade has been considered the main cause of the declines throughout the range of the species (CITES 2006). The Grey Parrot has been among the most traded of bird species listed on CITES Appendix II. Between 1975 and 2010 more than a million individuals were reportedly caught in the wild and exported from Africa (UNEP-WCMC 2014), but since estimates of mortality from capture to export vary from 30% to 66% (Fotso 1998b, a, McGowan 2001), these figure may rise to two million. BirdLife International (2014b) estimates that in some periods more than 20% of the wild population may have been harvested annually. Bans on the importation of wild-

caught birds into the USA and European Union, which were historically the largest importers, have coincided with a reduction in the number of export permits being issued (Martin et al. 2014). There is also, however, a large illegal trade that goes unreported and which is difficult to account for (Pires 2012). Moreover, Grey Parrots are traded within Africa as bushmeat and for medicinal/ceremonial purposes (Fotso 1998b, Adjakpa et al. 2002, Eniang et al. 2008). Grey Parrot was put on CITES Appendix II in 1975 (CITES 2015). In 2007, owing to concern about the effects of the large numbers of this species traded, a two-year ban was recommended for Cameroon and national quotas were set for Congo and DRC, although these are regularly exceeded (Martin et al. 2014).

1.6. Study site: The island of Príncipe

The island of Príncipe (1°32'-1°43'N 7°20'-7°28'E) lies 220 km off the coast of West Africa, in the Gulf of Guinea, and covers an area of 136 km^2 (c.17x 8 km) (Fig. 1.3). Formerly a Portuguese colony, it is now part of the Democratic Republic of São Tomé and Príncipe.
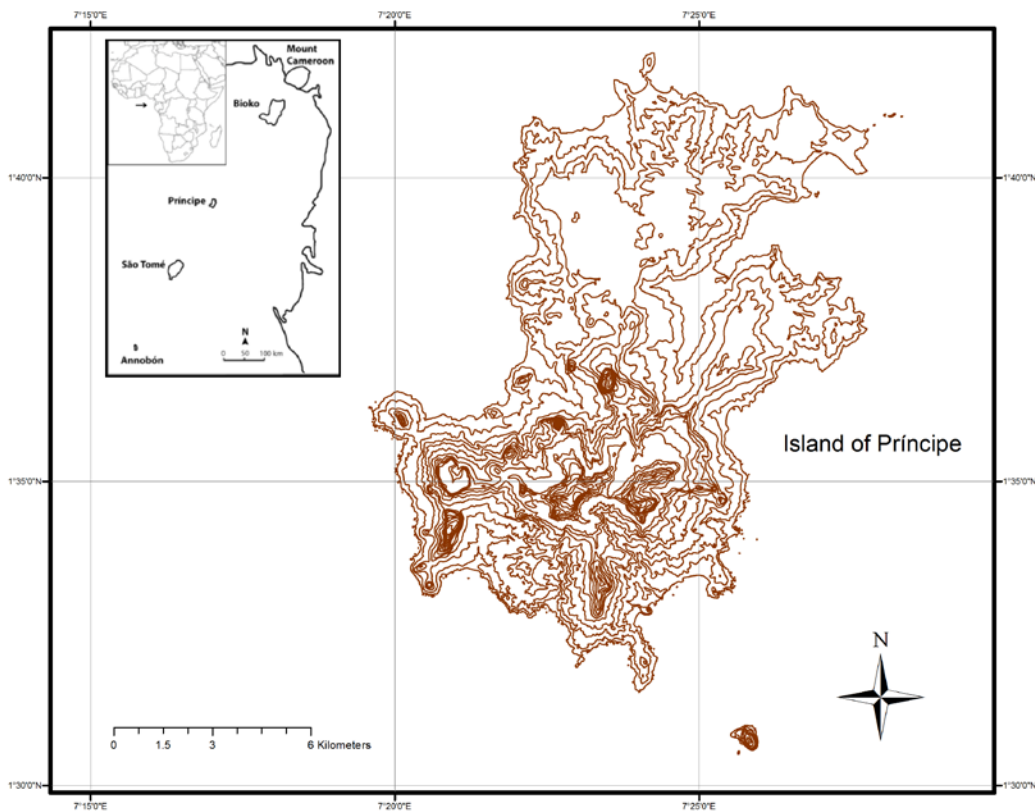
Figure 1.3. Orographic map of the Island of Príncipe and its position within the Gulf of Guinea.

1.6.1. Geology and geomorphology

Príncipe is part of a chain of Tertiary to Recent volcanoes which stretches across the Gulf of Guinea in a south-west direction for 1,600 km, and includes Bioko (Fernando Pó) and Mount Cameroon further north-west, and São Tomé

and Annobon further south-west (Jones and Tye 2006): the Cameroon Line (Fig. 1.4). Volcanic activity has been present since the Cretaceous and age progression in the line allows estimating the sub-aerial origin of Príncipe at 31 Ma (Figueiredo et al. 2011).
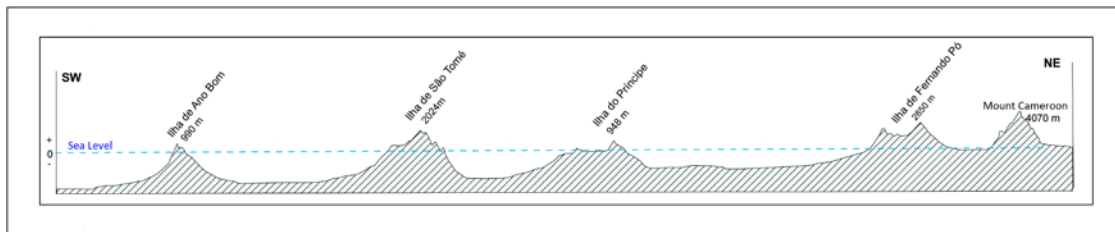
Figure 1.4. Topographic profile of the Cameroon Line (adapted from Tenreiro 1956).

Príncipe can be divided into two distinct regions: a relatively flat, low-lying basalt platform in the north, with hills below 180 m, and a mountainous central and southern region (Fig. 1.5). The highest peaks, Pico do Príncipe (948 m), Mencorne (935 m) and Carriote (830 m) are a topographic divide between the two regions (Jones and Tye 2006).
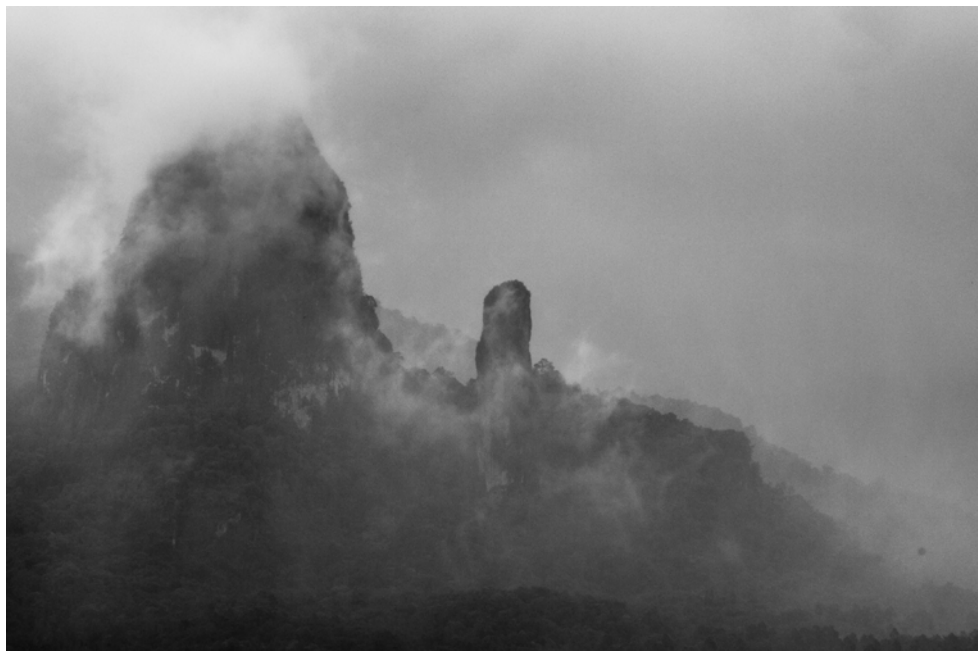
Figure 1.5. The central area of the island is dominated by steep mountains of volcanic origin.

1.6.2. Climate

The region has an oceanic equatorial climate regulated by the interaction of the southern monsoon winds from the Atlantic Ocean with the Intertropical Convergence Zone, defined by the northern dry *harmattan* wind from the Sahara desert (Diedhiou et al. 1999). The island of Príncipe intercepts the prevailing moist south-westerly winds throughout the year, so that rainfall in its south-western parts probably exceeds 5,000 mm/year (Bredero et al. 1977) (Fig. 1.6a). The rainy season lasts from September to May and the dry season (*gravana*) from July to August. A shorter dry season runs from December to early January (Fig. 1.6b). The north of the island is always drier than the south, and the south-western parts and high interiors are wet almost throughout the year (Jones and Tye 2006).
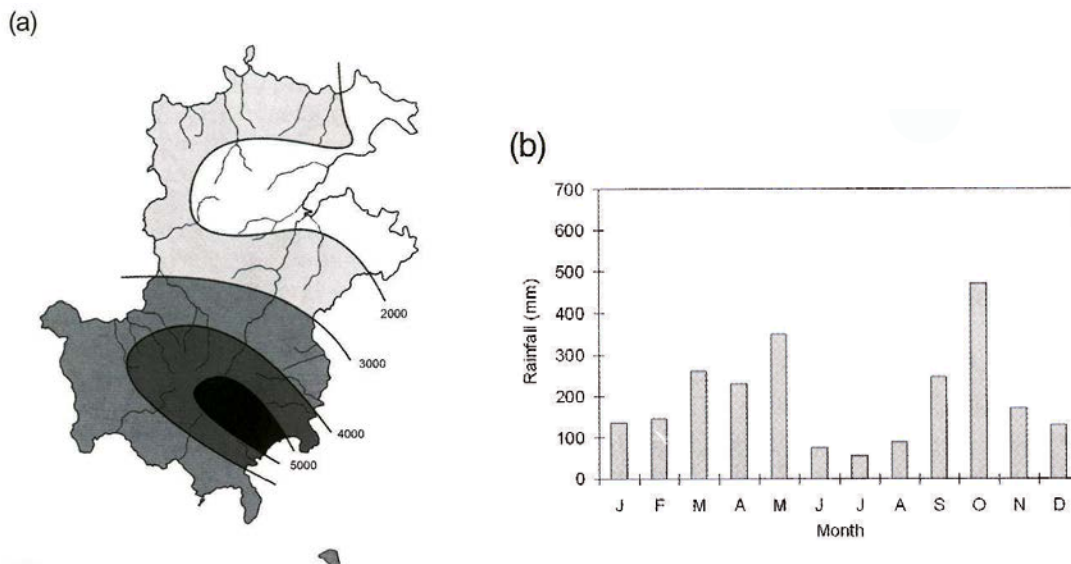
Figure 1.6. (a) Mean annual isohyets (mm) and (b) mean monthly rainfall on Príncipe (from Jones & Tye 2006).

1.6.3. Vegetation

The natural habitat of Príncipe has been described as rainforest (Exell 1944) or tropical moist broadleaf forest (Gascoigne 2004). The island was once entirely covered in lowland forest, but, after its discovery, all of the accessible areas

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were cleared and mainly planted with cocoa and coffee, and with coconuts and bananas in some areas. Although it has been said that all the primary forest had been cleared in 1906 in the attempt to eradicate sleeping sickness (Exell 1944), it is probable that most of the southern part of the island has been left untouched (Jones and Tye 2006).
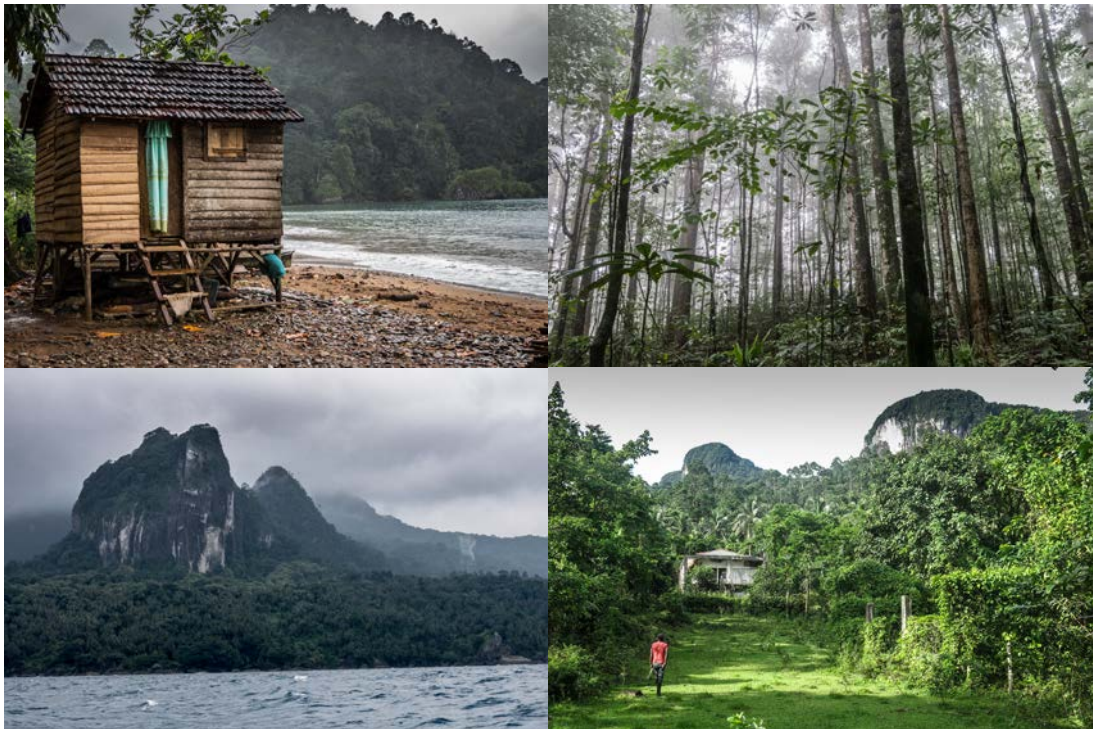
Figure 1.7. Fishing settlements have a minimal impact on surrounding forest habitats (top left Lapa). Large areas of primary forest (top right) remain in the southern half of the island thanks to its inaccessibility (bottom left as seen from the sea). Secondary forest has been rapidly claiming back vast areas where once there were large and productive plantations (bottom right Maria Correia). (All photos: S. Valle)

1.6.4. Biodiversity in the Gulf of Guinea

Príncipe is an integral part of the Guinean forests of West Africa biodiversity hotspot (Myers et al. 2000), and of the Congolian coastal forest ecoregion, one of the priority conservation areas identified by WWF (Olson and Dinerstein 2002). The island, like others in the Gulf of Guinea, holds high levels of

endemism at the species and generic level, and the conservation of these unique ecosystems has become subject of increasing international interest (Collar and Stuart 1988, Jones 1994, Peet and Atkinson 1994). Eight percent of angiosperm plant species in Príncipe are single-island endemics (Jones and Tye 2006). Endemic trees include *Rinorea insularis*, *Ouratea nutans*, *Casearia mannii*, *Croton stelluliferus* and *Erythrococca columnaris*. Príncipe is particularly rich in Euphorbiaceae, with five endemic species. Five out of the eight reptile species and all of the amphibians are endemic to the Gulf of Guinea islands, with two and one single-island endemics respectively (Fig. 1.8). Príncipe has an endemic subspecies of the African mainland shrew *Crocidura poensi* (De Balsac and Hutterer 1982). Four species of bat have been recorded from Príncipe, two are mainland forms, whereas a newly described subspecies of *Rousettus aegyptiacus* (*R. a. princeps*) and an undescribed new species of *Pipistrellus* are both endemic.

Figure 1.8. *Gastropyxis principis*, one of the two single-island endemic species of snakes in Príncipe (Photo: S. Valle)

1.6.5. Avian endemism

The island qualifies as an Endemic Bird Area (EBA) (Jones et al. 2001). Of 33 breeding landbird species, Príncipe has one monospecific endemic genus (*Horizorhinus;* recently suggested to be a clade of the *Sylvia* genus; Voelker et

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al. 2009, Voelker and Light 2011). Also present are six other single-island endemic species, in addition to four more shared with São Tomé and Annobón (Table 1). Additionally, six more mainland birds are represented by endemic subspecies in Príncipe (Jones et al. 1991). The recently split endemic Príncipe Thrush *Turdus xanthorhynchus* (Fig. 1.9) is of particular conservation concern owing to its extremely small population restricted to small range (Dallimer et al. 2010, Melo et al. 2010). Although information on other Príncipe endemics is scarce, most species are believed to be reasonably abundant (BirdLife International 2014a).

Figure 1.9. The Critically Endangered Príncipe Thrush *Turdus xanthorhynchus* (Photo: L. Crellin)

Table 1.1. The endemic bird species of Príncipe, whether they are single-island endemic (–) or shared with São Tomé (ST) and/or Annobón (A), and their most recent conservation status according to BirdLife International (2014a).

Species	Endemism	Status
São Tomé Bronze-naped Pigeon *Columba malherbii*	ST, A	NT
São Tomé Spinetail *Zoonavena thomensis*	ST	LC
Príncipe Kingfisher *Corythornis nais*	–	LC
Príncipe Thrush *Turdus xanthorhynchus*	–	CR
Dohrn's Thrush-babbler *Horizorhinus dohrni*	–	LC
Príncipe Sunbird *Nectarinia hartlaubii*	–	LC
São Tomé White-eye *Zosterops ficedulinus*	ST	VU
Príncipe Speirops *Speirops leucophaeus*	–	NT
Príncipe Glossy Starling *Lamprotornis ornatus*	–	LC
Príncipe Golden Weaver *Ploceus princeps*	–	LC
Príncipe Seedeater *Serinus rufobrunneus*	ST	LC

1.7. Overall aim of the PhD and overview of the chapters

The overall aim of this PhD thesis is to better understand the population ecology of the Grey Parrot in Príncipe, and to use this as a model to explore new ways of studying, conserving and managing, this and other heavily harvested parrot species elsewhere. In order to do this, several aspects of the parrot's ecology

and population dynamics were investigated and the relevant results are presented in the following chapters.

Chapter 2: Seasonality in habitat use by the superabundant Grey Parrot Psittacus erithacus on Príncipe, Gulf of Guinea

Wild populations of Grey Parrot are declining over much of the range under the pressure of habitat loss and the harvest for the pet trade. Despite the species' popularity and high value on the market, little is known about its densities and habitat preferences in the wild. Grey Parrot population was estimated on the island of Príncipe, for two different seasons (i.e. post-breeding and pre-breeding). Local abundance was also estimated to investigate how this varied in relation to different habitat features and to different the time of the year. Population densities are given and compared to the information available from elsewhere in the species range, and from other parrot species. The implications of seasonal variations in habitat use are discussed both from a survey design and conservation management perspective.

Chapter 3: Testing simple methods for effective abundance estimation and monitoring in parrots

Estimating parrot densities poses various challenges. A summary of the available and most used methods is given in this chapter, and three novel survey methods are tested, as possible proxies for parrot densities, where more accurate methods are not applicable due to limitations in time and resources. Accuracy of the two low-cost methods, namely simple encounter rate and counts from vantage points, as possible proxies of local abundance is tested. Their advantages and limitations are discussed. Moreover counts along habitual flyways, are compared with results from distance sampling, to explore their potential as a possible method for long term parrot monitoring.

Chapter 4: Exceptionally high breeding density and output in an island population of the heavily-traded Grey Parrot Psittacus erithacus

Little is known about Grey Parrot nesting ecology and requirements, although it is likely that these may be limiting factors as they are for other parrot species. In this chapter, nests and nesting habitat characteristics in Príncipe are analysed and the possible effect of the latter on productivity is investigated. A minimum nest density is also estimated for the island. Results are compared to known parrot nest densities and the likely causes are discussed as well as implication for the species' conservation and management.

Chapter 5: Using scenarios to predict effects of harvest and habitat loss on a population of Grey Parrots Psittacus erithacus

Population Viability Analysis (PVA) is a useful tool for modelling population dynamics in the face of possible threats. A PVA model is built to study Grey Parrots on Príncipe, and understand the species' sensitivity to the harvest for the pet trade and habitat loss. The model is used retrospectively to understand the likely trajectory of Príncipe's population in the last 20 years and infer on its causes. A sensitivity analysis is performed to investigate which life history traits are most crucial for the species' survival. The model is then used to investigate a number of hypothetical future harvest and habitat change scenarios. The possible sustainability of different harvest techniques and quotas, as well the consequences of habitat loss are discussed in the light of the outputs obtained from the models. Finally, the possible interaction of these threats with each other, and how this may affect the population is explored. The relevance of the results for conservation and management is discussed, highlighting advantages and limitations of the PVAs as a tool for the study of threatened parrot populations.

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Chapter 2. Seasonality in habitat use by the superabundant Grey Parrot *Psittacus erithacus* on Príncipe, Gulf of Guinea

2.1 Summary

There is grave concern for wild populations of Grey Parrot *Psittacus erithacus* due to the combined pressures of habitat loss and harvest for the pet trade, and yet, very little is known about its densities and habitat preferences. Line transect distance sampling was used to estimate local post-breeding and pre-breeding population densities of grey parrots in 42 one km^2 units on the island of Principe. Local densities were related to a range of habitat features within the squares using General Additive Models (GAMs). Population densities averaged 48 ± 3 (SE) in the pre-breeding, and 59 ± 4 individuals km^{-2} in the post-breeding season, extremely high as compared to abundance elsewhere within the species' huge range. Despite Príncipe's small size (139 km^2) and large parrot population (6-8,000), parrots were not recorded in around one quarter of squares surveyed. Local abundance changed seasonally, with densities being significantly higher in secondary than primary forest in the post-breeding but not the pre-breeding season. Local pre-breeding abundance was most strongly related to presence of nest tree species, but post-breeding season distribution was most strongly tied to presence of feeding tree species and forest on lightly sloping ground. It is highlighted 1. the importance of preserving a matrix of habitat types to provide resources for parrots during different seasons, and 2. the need to consider carefully timing of parrot surveys, as, even on this small island, seasonality in use of different areas and habitats, can be significant.

2.2   Introduction

Parrots (Psittacidae) are among the most endangered bird families in the world, with 37% of all species listed as threatened or 'Near Threatened' (IUCN 2014). Excessive capture for the international pet trade coupled with habitat degradation and loss are considered the main causes of worldwide parrot population declines (Collar and Juniper 1992, Snyder et al. 2000). However, despite their endangered status, often little is known about the size of populations in the wild (Marsden and Royle 2015), their habitat requirements (Snyder et al. 2000), and, especially how these may change seasonally (Renton 2002).

Parrot habitat is defined by a number of limiting elements, namely food (Saunders 1990, Berg et al. 2007), nest-sites (Beissinger and Bucher 1992, Munn 1992, Wiebe 2011), roost-sites (Chapman et al. 1989), and water and mineral licks (Lee et al. 2010), the availability of which can vary in space and time. Moreover, some habitats close to the main range may provide crucial resources at critical times of the year (Foster et al. 1980). As a consequence many parrot species have evolved to be highly mobile, capable of travelling long distances and often showing marked periodical variations in their diet (Saunders 1980, Renton 2001). In some species, this results in a regular periodical migratory behaviour (e.g. Swift Parrot *Lathamus discolor* and Orange-breasted Parrot *Neophema chrysogaster*, Chan 2001). While this ecological flexibility has allowed some parrot species to adapt well to habitat alterations (Marsden 1998, Bonadie and Bacon 2000, Vaughan et al. 2006), others remain highly specialized in their foraging niches (Roth 1984, Matuzak et al. 2008) and require careful investigation to provide a robust evidence base for their long-term management. However, despite this increasing perception that parrots require a variety of habitats and forest types to sustain healthy populations (Marsden and Pilgrim 2003), ranging patterns of psittacines are understudied and poorly understood (Renton 2002). Identifying the environmental drivers of abundance and understanding how these change with periods is a priority, as periodical habitat association studies have been largely used for the formulation of practical conservation and management policies (Fielding and Haworth 1995, Marsden and

Fielding 1999, Boitani and Fuller 2000). This approach has also been particularly useful in understanding potential responses to habitat disruption (Smith et al. 2001, Gunnarsson et al. 2006).

Surveys aimed at measuring abundance and range size are the base of any evaluation of extinction risk and, in turn, of the prioritization of conservation effort (Mace et al. 2008). Seasonal changes in habitat use may have important repercussions on surveys results, and in turn on population estimates, if their timing is not chosen suitably. For example, results from roost counts can be biased as the use of communal roosts can vary substantially throughout the year (Cougill and Marsden 2004), and prior to the breeding season as birds may start roosting in nest holes (Saunders 1979). Distance sampling is among the most accurate population estimate methods currently used by parrot ecologists (Walker et al. 2005), but is most efficient when birds are spread relatively evenly through the study area in time and space (Buckland et al. 2005). Particular caution is needed in deciding the timing of surveys of most tropical forest birds, as seasonal differences in calling rates, home range size, short-term movements in response to shifts in resources availability, and differential habitat use can all affect detectability, and therefore precision and accuracy, of distance sampling estimates (Buckland et al. 2008). Seasonal change in relative abundance parrot species has been documented for a number of species (Brightsmith 2006, Lee and Marsden 2012). For the same reason, for monitoring purposes, it is important that subsequent yearly counts should be carried out at similar times of year, and data should not be compared if habitat alteration may have changed the species' detectability between years (Marsden 1999). There can be no easy rules about choosing the timing of surveys, and only a better understanding of as species differential use of their home range and habitats can result in better designed surveys (Bibby et al. 1998).

The Grey Parrot *Psittacus erithacus* has just recently been up-listed to 'Vulnerable' owing to the rapid population decline registered all across its wide African distribution range in the last 50 years (BirdLife International 2014). As for many other parrot species the causes of such a dramatic drop are to be found in a combination of constant habitat destruction and the very poorly regulated harvest for the

international pet trade (IUCN 2014). Despite its popularity and its commercial value on the international pet market (CITES 2006), information on the size and densities of wild populations, local movements and seasonality in habitat requirements, remains poorly known. The island of Príncipe is a small island (Fig.1) in the Gulf of Guinea (West Africa), and it is home to a healthy population of Grey Parrots despite a long tradition of parrot harvesting and trade (Juste 1996, Marsden et al. 2013), offering an exceptional opportunity to study the species in a 'closed' system.

The objectives of this study were: 1. to estimate abundance of grey parrots, and to examine how population densities vary spatially and seasonally; 2. to understand how local parrot abundance is linked to habitat characteristics and how these habitat associations change seasonally; and, 3. to explore the implications of the above for conservation management and design of surveys.

2.3   Methods

2.3.1 Study area and species

The island of Príncipe (1°32' - 1°43' N, 7°20' - 7°28' E; 139 km^2) lies 220 km off West Africa, in the Gulf of Guinea (Fig. 1). Príncipe can be divided in two distinct regions: a relatively flat, low-lying basalt platform in the north, with hills below 180 m, and a mountainous central and southern region (Jones and Tye 2006). By the beginning of the 20th century the original forest in the former had been deeply modified in many places by clearance, selective felling and the creation of cocoa, coffee and coconut plantations (Exell 1973), while the centre/south still remains covered in pristine forest rich in floristic endemics (Jones 1994, Figueiredo et al. 2011). The island intercepts moist south-westerly winds throughout the year, so that rainfall in its south-western parts probably exceeds 5000 mm yr^{-1} (Bredero et al. 1977). The rainy period goes from September to May and the dry period (*gravana*) from July to August, while a shorter dry period is from December to early January, with the north being always drier than the South (Jones and Tye 2006).

2.3.2 Population and density estimates

The island was divided in 133 one-km^2 grid squares based on the Universal Transverse Mercator (UTM) geographic coordinate system. These were then classified as primary or secondary forest, according to the latest vegetation surveys (Albuquerque et al. 2004), and ground-truthing. Fifty-nine squares (44%) were assigned to the primary forest habitat category. The remaining 74 squares (56%) fell into the secondary forest category, which included lowland forest (26 %), as well as overgrown cocoa *Theobroma cacao* plantations (31%), coconut palm *Cocus nocifera* groves (29%), and oil palm *Elaeis guineensis* estates (11%). Forty-one squares (12 in primary and 29 in secondary forest) were selected systematically on a map (i.e. one every five), nonetheless owing to accessibility constraints and safety reasons, the nearest accessible square had to be visited instead (Fig. 1).
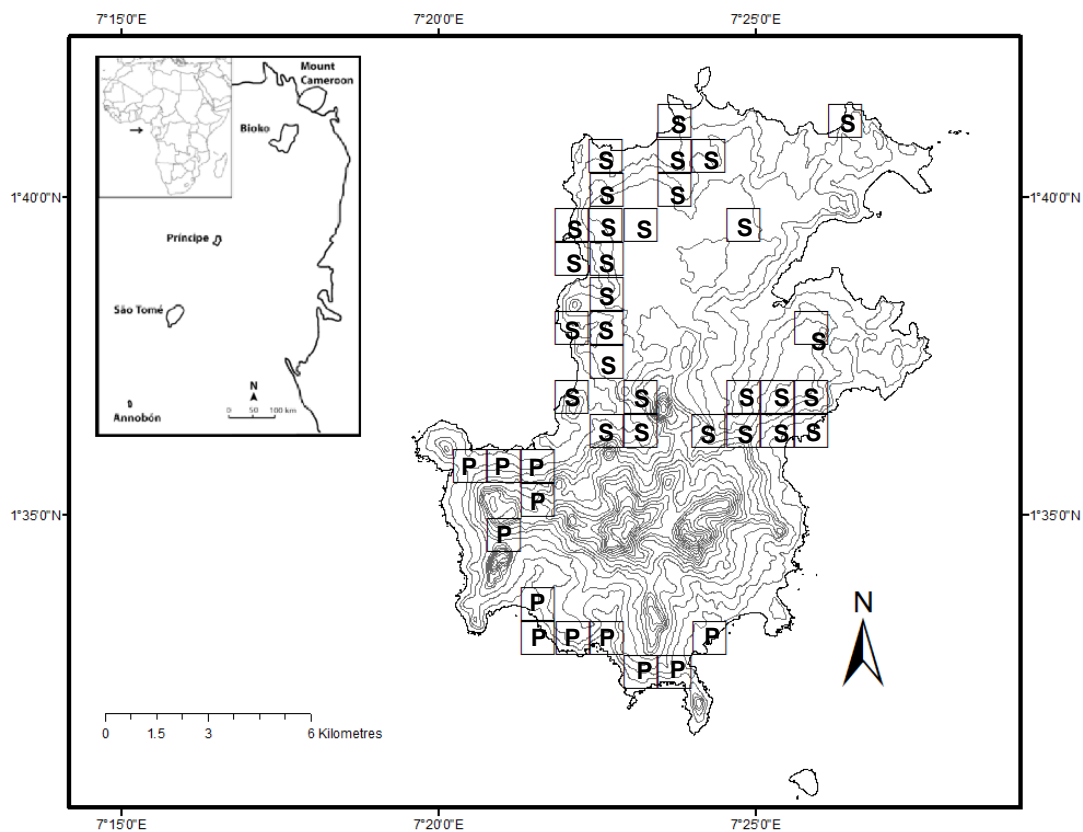
Figure 2.1. Orographic map of Príncipe and its position within the Gulf of Guinea, and the locations of 41 surveyed 1-km^2 sample grid squares i.e. 12 in primary (P) and 29 in secondary forest (S) (see § 2.4.2 for selection method).

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In each grid square, a transect of variable length (mean 1 km ± 0.4 (SD) was walked at a slow pace (ca. 1 km h^{-1}). Since steep terrain and dense vegetation prevented safe navigation, only possible routes through the vegetation or existing paths of width < 0.5 m, were used. All Grey Parrots heard and seen perched within 50 m of the transect route were counted, and their horizontal distance from the transect line measured with a laser range-finder. All flying birds were excluded from the counts unless they had been flushed and their take-off point identified (Marsden 1999). Transects were walked between 07h00 and 11h00, when parrot activity is known to be high (Blake 1992). All counts were conducted by SV alone, in the absence of rain and strong wind). Transects were initially walked once after the fledging period (March–April 2014; 'post-breeding') and again just before the following breeding season (August–September 2014; 'pre-breeding').

DISTANCE 6.0 (Thomas et al. 2010) software was used to estimate grey parrot density (individuals km^{-2}) in each of the surveyed grid squares using a shared detection function across squares. A measure of forest regeneration (see § 1.3.3) was included as a transect-specific covariate in the Multiple Covariates Distance Sampling (MCDS) engine as it was believed to be likely to affect detectability (Marques et al. 2007).A multiple covariates distance sampling analysis was performed with a hazard-rate function and cosine adjustment term. Parrot sightings were entered as clusters (i.e. number of birds seen or heard with certainty in a group) with exact measured distances rather than distance ranges. In order to eliminate outlying records which contribute little to the calculated detection function and may affect model fitting (Buckland et al. 1993), all observations beyond 50 m were discarded. Distance data were assigned to five equal intervals for analyses. Optimal detection function was selected using the lowest Akaike's Information Criterion (AIC; Akaike 1974). Variance was estimated by bootstrap resampling (999 resamples). The same analysis returned an estimate of the Grey Parrot population for the island.

2.3.3 Habitat characterization

Every 500 metres along each transect, the following habitat measures were taken within a 20 m radius sample plot: geographic coordinates and altitude (GPS); slope (clinometer); aspect (compass); maximum canopy height (clinometer and range finder); canopy closure in five equidistant points (type-A spherical densitometer; Jennings et al. 1999); number of woody stems at 1 m height (counted by swinging a 1-m-long stick through 360° at the same height, and hereafter referred to as 'regeneration'); and diameter at breast height (dBH) of the three biggest-girthed trees (tape measure; White and Edwards 2000); and estimated percentage of ground covered by grassy vegetation, estimated by eye (hereafter 'ground flora'). All these measures were then averaged across sample plots to give a single value per square. Presence or absence in each sample plot was recorded for all tree species which, from literature and local knowledge, Grey Parrots were known to feed on or nest in (Table 1), and for a set number of widespread introduced/cultivated tree species as an indicator of anthropogenic disturbance (Lee and Marsden 2008). For each square, the proportion of vegetation sample plots in which each of the above tree species was present, was calculated, and this, in turn was averaged for the feeding, the nesting, and the introduced/cultivated species. In two grid squares transect length was <500 m, so they were excluded from any further habitat association analysis as no vegetation sampling had been carried out.

2.3.4 Seasonality in parrot-habitat associations

Differences in density between primary and secondary forest within and between periods, were tested using the Mann-Whitney U test, and variation in density estimates within squares between the two seasons examined with Spearman's Rank Correlation Analysis. To investigate the relationship between local density and habitat characteristics, Random Forests (henceforth 'RF') was used to identify most likely predictors of local density among all habitat variables (Cutler et al. 2007). RF is a decision-tree modelling technique designed to identify nonlinear associations

among multiple correlated predictor variables (Breiman 2001). RF has been shown to have higher predictive capability compared to alternative statistical techniques (Prasad et al. 2006, Cutler et al. 2007). RF models were built of 100,000 classification trees, and variables were considered important if their variable importance score were above the absolute value of the lowest negative-scoring variable (Strobl et al. 2008). Selected variables were then used as independent variables in Generalized Additive Models (GAMs) to explore how more exactly they were linked to parrot density. In modelling parrot density as a function of slope, data from two outlying plots (i.e. ≥ 30°) were not included in the analysis. All statistical analysis was performed with R software RF models and GAMs were done using 'party' and 'mgcv' packages respectively (R Core Team 2014).

2.4   Results

2.4.1 Population size and density estimate

The total number of detections did not vary greatly between the two seasons, and in each one of them, parrots were detected in the majority of the surveyed squares (χ^2 = 2.07, df = 1, p<0.05), with no particular inclination for either type of forest (χ^2 = 2.98, df = 1, p = 0.08, Table 1). Hazard-rate key function with cosine adjustment term provided the best fit to the data both for pre- and post-breeding season). Results for the population estimates are summarised in Table 1.

Table 2.41. Summary of the distribution of parrot detections across forest types in the two seaseons.

Season	Total no. of detections	Number of squares			
		With detections	*With no detections*	*in primary forest*	*in secondary forest*
pre-breeding	125	26	15	5	21
post-breeding	139	24	17	4	20

Table 2.42. Results of the Distance sampling analyses for the pre- and the post-breeding seasons.

	Pre-breeding season	**Post-breeding season**
Mean density (parrots km^{-2}) ± SE (95% CI)	47.9 ± 2.7 (43.7 – 54.5)	58.78 ± 4.2 (53.2 – 66.6)
Total population (parrots) ± SE (95% CI)	6,517 ± 361 (5,940 – 7,409)	7,996 ± 568 (7,241 – 9,065)
Minimum density (parrots km^{-2}) excluding 0	16.14 ± 0.9	17.62 ± 1.3
Maximum density (parrots km^{-2}) ± SE	154.06 ± 8.24	335.62 ± 23.73
Effective strip width of detection (m) ± SE (95% CI)	50.0 ± 0.7 (48.59 - 51.44)	48.1 ± 1.0 (46.03 - 50.38)
Mean cluster size (parrots) ± SE (95% CI)	1.65 ± 0.09 (1.47 – 1.85)	1.73 ± 0.08 (1.58 – 1.9)

Eighteen and seventeen grid squares had no records in the pre- and post-breeding season respectively, with 12 of these (5 in primary and 7 in secondary forest) having zero densities in both seasons. In the pre-breeding season only three grid squares had a density between 100 and 200 parrots/km^2 (max ± SE = 154.06 ± 8.24; Fig.2a), but in the post-breeding season four grid squares did so, and three had a density ≥ 200 parrots/km^2 (max ± SE = 335.62 ± 23.73; Fig. 2b).
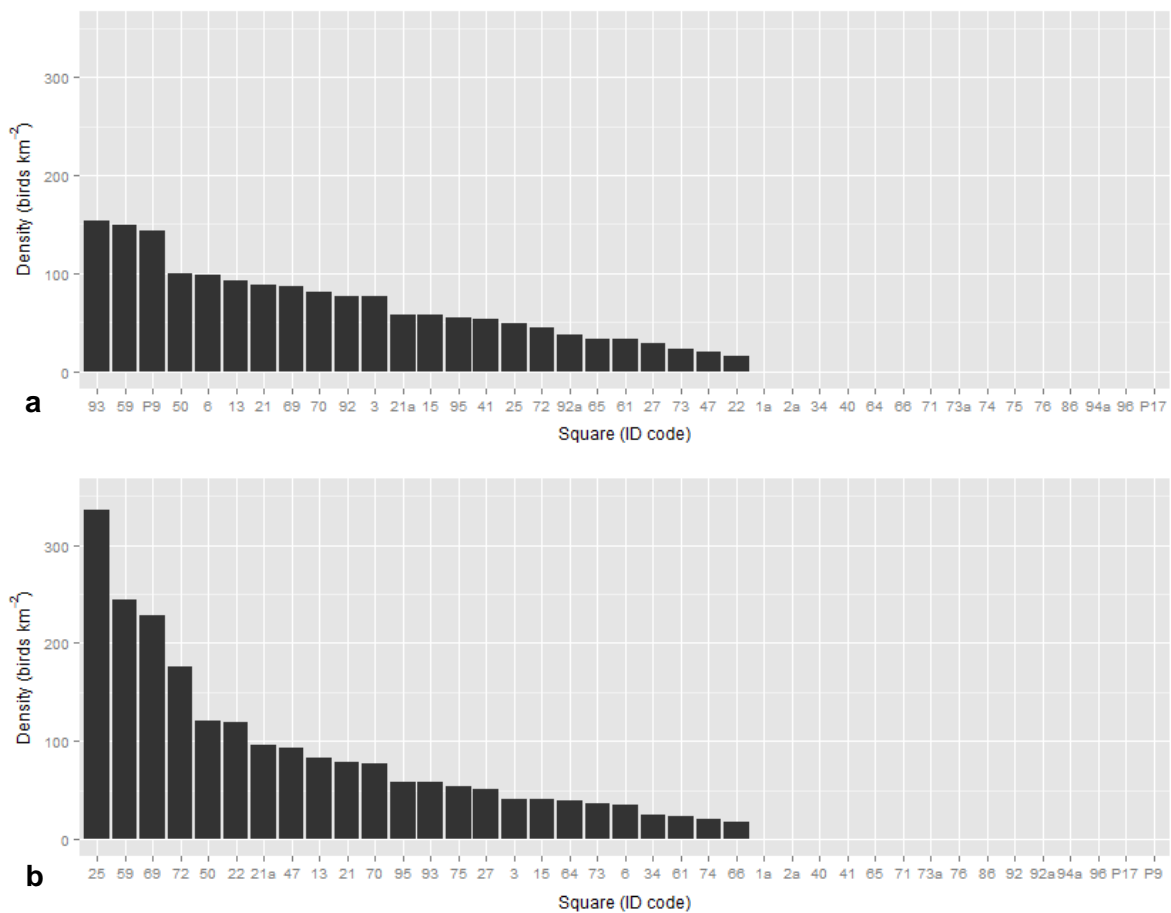
Figure 2.2. Distribution of densities across squares in pre- breeding (a) and post-breeding seasons.

Parrot density was significantly lower in primary than in secondary forest in the post-breeding season (W = 64, p < 0.01), but there was no significant difference in the pre-breeding season (W = 139, p = 0.85). There was no systematic difference (i.e.

increase or decrease) in density within the 41 grid squares (W = 260, p = 0.36), between pre- and post-breeding season. There was considerable variability in densities within squares across the two seasons (Fig. 3).
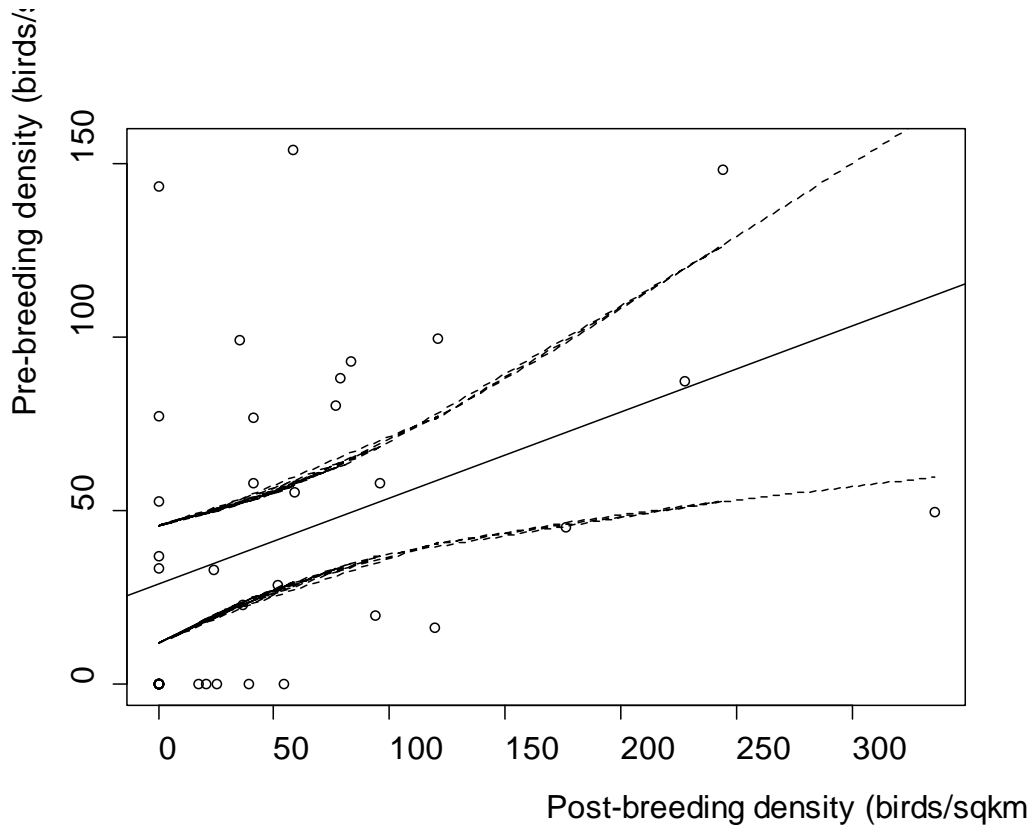
Figure 2.3. Correlation between pre- and post-breeding densities with 95% confidence interval.

2.4.2 Seasonality of parrot-habitat associations

RF analyses indicated that the presence of nest tree species was the best predictor in the pre-breeding season, while terrain slope and presence of food trees were the two major predictors of parrot density in the post-breeding season (Fig. 4).
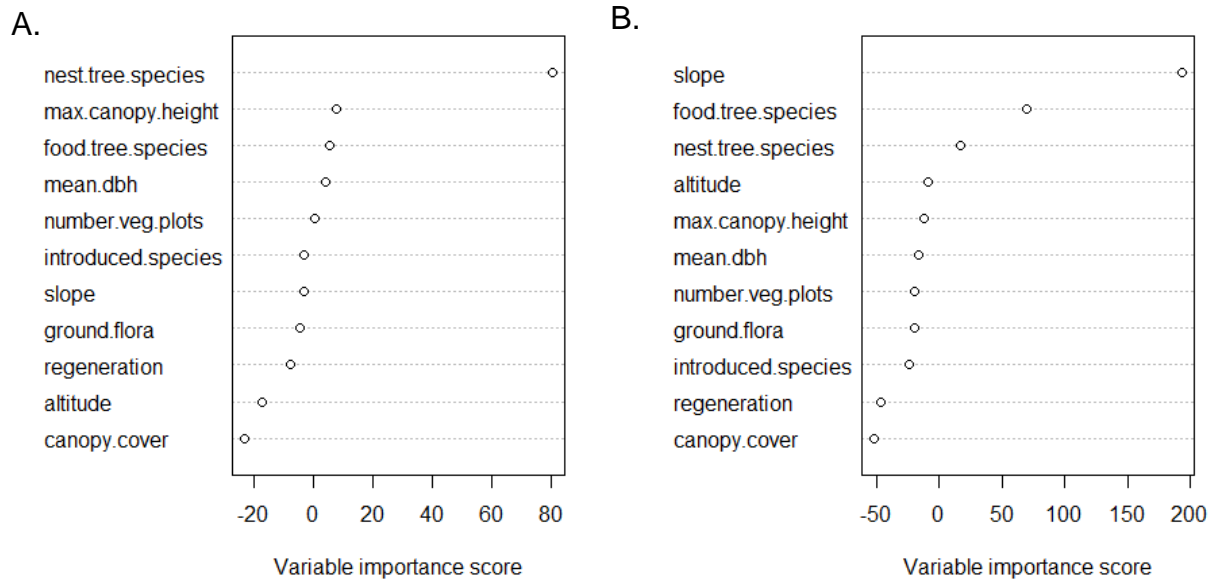
Figure 2.4. Dotchart of importance variables measured as percentage increase in mean Standard Error (%IncMSE) after each tree permutation for A. pre-breeding and B. post-breeding seasons.

In the pre-breeding season, the presence of nest-tree species was not a significantly strong predictor of parrot density. Nonetheless, densities were nonlinearly correlated with the probability of finding nest-tree species with a minimum of 11% needed (F=2.99, p=0.07; Fig. 4).
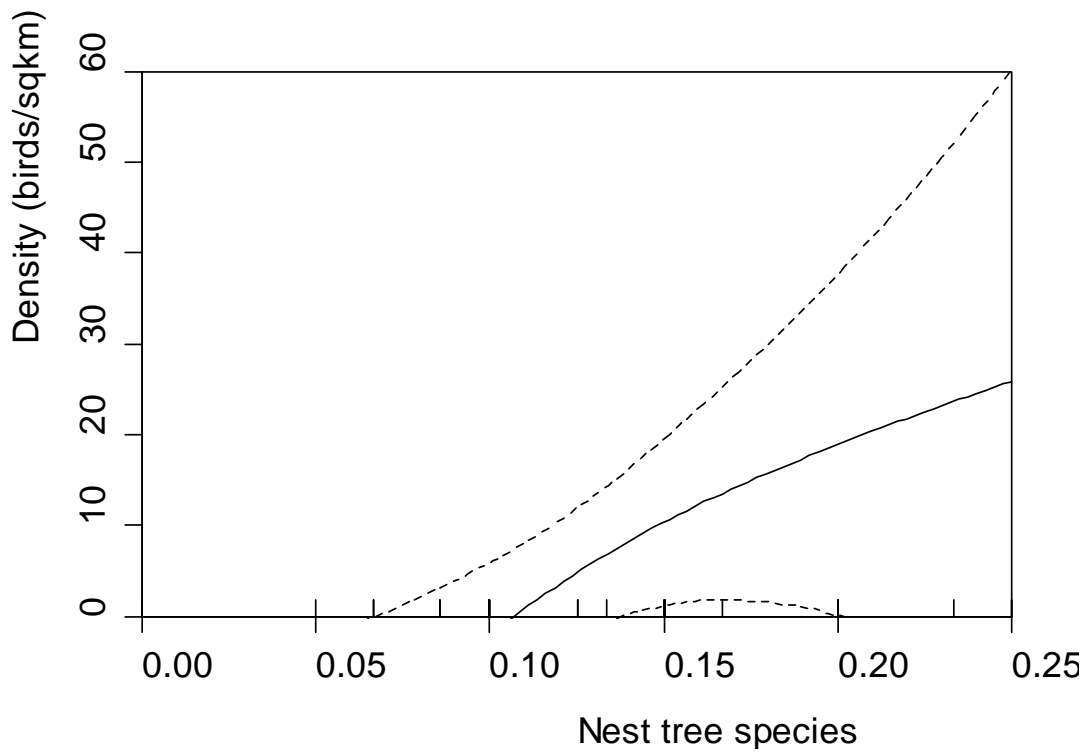
Figure 2.5. Grey Parrot density in relation to the probability of finding nest tree species in the pre-breeding season (continuous line) with 95% confidence interval (dashed line).

In the post-breeding season, local density was related to slope in a nonlinear way, with gently sloping terrain (0–20°) associated with high densities (F=3.0, p<0.05, Fig. 5a), and linearly with presence of feeding trees (F=8.04, p<0.01, Fig. 5b). There was no correlation between terrain slope and the presence of feeding species (r_s = +0.08, p = 0.63, n = 39).
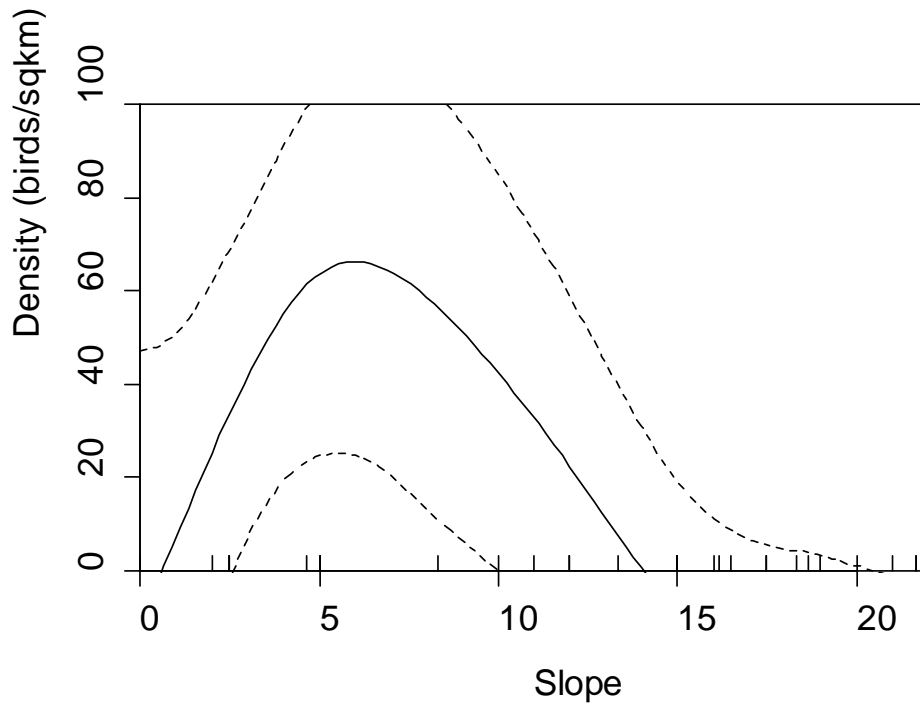
a.
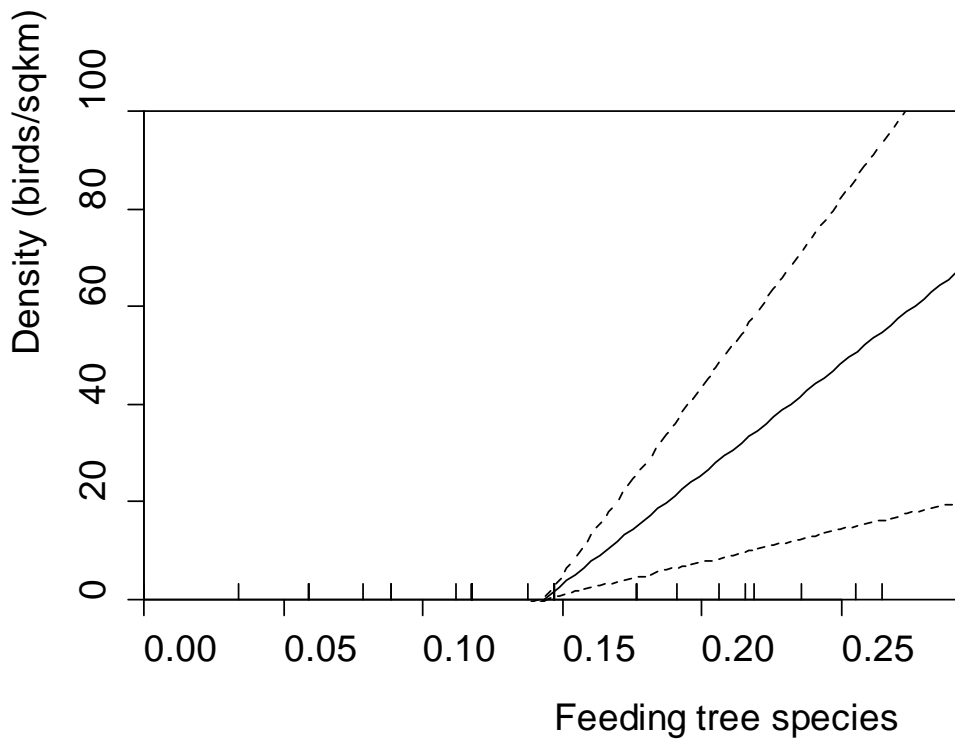
b.

Figure 2.6. Relationships, from GAMs, between Grey Parrot density and a. slope, b. the probability of finding food tree species, in the post-breeding season (continuous line) with 95% confidence interval (dashed line).

2.5   Discussion

At around 48–59 individuals km^{-2}, estimated Grey Parrot densities on Príncipe were extraordinarily high compared to those reported elsewhere, with 0.15–2.2 birds km^{-2} in Ghana (Dändliker 1992) and 4.9–6.0 birds km^{-2} in Nigeria (McGowan 2001), although caution is needed as estimate methods differed. Recent density estimates performed with distance sampling in Cameroon also show densities much lower than in Príncipe, with the highest being 29 and 10.7 birds km^{-2} in Lobeke and Campo Ma'an National Parks respectively (Marsden et al. 2013). Densities are high even when compared to other species of parrot. Out of 90 parrot species for which at least one density estimate is available, only 17 have densities higher than 50 birds km^{-2}, and all but two (Red-faced Parrot *Hapalopsittaca pyrrhops* and White-crowned Parrot *Pionus senilis* in Ecuador) are insular populations (Marsden and Royle 2015). This may be the consequence of a combination of particular environmental conditions, as well as of the 'density compensation' effect, where the summed high population densities of the few species on islands is similar to the summed lower densities found on species-rich mainland (MacArthur et al. 1972). Príncipe may therefore be serving as a stronghold for the otherwise declining global population of Grey Parrots, as other islands are for other parrot species (e.g. the Bolama-Bijagós Archipelago for the Vulnerable Timneh Parrot *Psittacus timneh*; Clemmons 2003).

The similarity of the pre- and post-breeding density estimates may reasonably be considered evidence that distance sampling is a good method for estimating population densities, and provides highly comparable results, regardless of their accuracy. Results from post-breeding surveys may be inflated by the newly recruited juveniles, thus the pre-breeding season may be more appropriate timing for estimating the effective population size. Estimates may also differ between seasons owing to behavioural traits e.g. an increase in detectability owing to the presence of juveniles in the post-breeding, or a decrease due to pairs securing nest-sites in the pre-breeding.

Despite parrots being highly mobile birds (Collar 1997, Juniper and Parr 2003), the island of Príncipe being relatively small, and the Grey Parrot population exceptionally abundant, there were still some areas which, in both seasons, did not hold any

parrots (i.e. 36% of surveyed grid squares). This shows that some areas are permanently, or seasonally, devoid of any attraction of the species (e.g. food), suggesting some precise habitat requirements. Several parrot species are known to have evolved specialised diets to reduce competition with other sympatric species of the same family or other frugivores (Wirminghaus et al. 2001, Matuzak et al. 2008, Montes and Verhelst 2011). Importantly, in the post-breeding season, there were a few grid squares, in secondary forest, which had very high densities (i.e. ≥ 200 parrots). These areas, owing to their environmental characteristics, are likely to periodically host high concentrations of important resources (e.g. fruiting trees), as confirmed with the correlation found with food tree species. Such large densities, could also be attributable solely to the influx of newly fledged juveniles, but it may also suggest some more complex post-breeding behaviour, as some parrot species are known to establish crèches as an anti-predator behaviour or for flight training (Rowley 1980, Wanker et al. 1996, Taylor and Perrin 2006).

Moreover results from this study suggest that the already patchy distribution also has a clear periodical variation. Parrot aggregations are known to vary significantly between seasons with the availability of the preferred food sources (Galetti 1997), and crop raiding is an extreme example of this behaviour (Bucher 1992). Changes in the extent of occurrence and accessibility resources are known to result in periodical variations in abundance of several parrot species, ranging from opportunistic changes in distribution (Renton 2001), to proper migratory movements (Chan 2001). Consistent with our results, distributional opportunism is known to be often restricted mainly to the non-breeding season (Forshaw 1989).

The periodical variation in habitat preference also has cautionary implications for survey design. Particular care is recommended, when deciding the timing and location of any survey (Bibby et al. 2012). This applies particularly to the study of tropical birds, as calling rates, home range size, short-term movements in response to food availability and participation in mixed-species foraging flocks may all affect accuracy and precision of density estimates (Buckland et al. 2008). Owing to Príncipe's small size, it was possible to carry out surveys in a relatively large proportion of the total study area, averting the risk of under- or over-estimating the

population size due to seasonal variability. Nonetheless, most ecological studies, because of limited resources, sample a very small proportion of their study area, so that choosing inadequately the timing of survey or the sampling areas may result in great inaccuracy in the estimates (Buckland et al. 2005).

In the pre-breeding season there seem to be a movement of birds towards areas with high numbers of nest trees. Grey Parrots, like the majority of parrots nest in natural tree cavities, to which they may make only minor adaptations (Collar 1997), and the availability of nest sites is known to be a crucial factor in parrot breeding success (Beissinger and Bucher 1992). Thus, it is likely that parrots, which are known to form long term-pair bonds on the basis of complex behavioural rituals (e.g. allopreening and allofeeding) (Juniper and Parr 2003), may be starting to secure a mate and a nesting site long before the laying dates. In post-breeding season, Grey Parrots preferred areas with intermediate levels of slope and good availability of food resources. The influence of slope on biodiversity has seldom been tested, although relationship between slope and plant diversity has indirectly been reported before (e.g. Maurer et al. 2006). Good quality forest is likely to be found at mid-levels of slope, as vegetation is more likely to be affected by anthropogenic disturbance on flat ground, and to struggle to grow, due to the soil quality, at steeper slopes (McIntyre and Lavorel 1994). Thus, despite the fact that no correlation was found in this study, a link between slope and presence of food trees is likely. Food availability may also be particularly crucial in the post-breeding season, owing to the developmental needs of the newly fledged juveniles; their first 3-4 months are known to be characterised by very low survivorship (Young et al. 2012), and high dependency on parental care (Benson et al. 1988).

Príncipe holds an extremely large Grey Parrot population within a small area and yet birds seem to have a very patchy distribution. Moreover, habitat preferences appear to shift predictably in different periods of the year. These shifts are likely to be linked to spatial variability in habitat and to how resources provide for birds during different stages of their life cycle. The variability in bird densities and distribution in such a small range of space and time emphasizes the importance of selecting suitable timing and sample areas in the design of a survey aiming at estimating parrot

population size and densities (Buckland et al. 2008). Moreover these results highlight how conservation management plans directed at the preservation of parrot species may have to take into serious consideration periodical changes in habitat preferences, and the preservation a matrix of habitats much more diverse than previously thought (Law and Dickman 1998).

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Chapter 3. Testing simple methods for effective abundance estimation and monitoring in parrots

3.1. Summary

Estimating and monitoring population sizes of the highly threatened parrots would provide valuable insights into their conservation status. Ideally, density estimates for any species would be derived from a standardised method such as distance sampling, but their parrots' patchy distribution, variable abundance, cryptic habits and high mobility, along with logistical difficulties and scarcity of local resources often present major obstacles to their effective study. Three simple and inexpensive methods (namely encounter rate, long watches and flyway counts) were empirically tested as possible surrogates for more technical density estimates and monitoring methods, using grey parrots *Psittacus* spp. as a model species. Firstly, line transect distance sampling and a simple encounter rate method were carried out at ten sites across five West and Central African countries. Density estimates were highly variable across sites, ranging from 0—0.5 birds km-2 in Côte d'Ivoire and central D. R. Congo to over 30 birds km-2 in Lobéké National Park (Cameroon) and over 70 birds km-2 in parts of the island of Príncipe. Most significantly, a relationship between grey parrot densities estimated from two methods was identified, with important implications on the possibility of monitoring this species, or other parrots, with large distribution ranges despite the logistic limitations. Secondly, long watches were performed over two different season from nine vantage points overlooking patches of forest of variable size on the island of Príncipe. The number of outbound and total flights of Grey Parrots in the areas were recorded in different time slots throughout the day, and a possible relationship with the densities estimated in the same areas with distance sampling was investigated. A weak relationship was found only with outbound flights recorded in the last three hours of the day, and only for small areas (i.e. where detectability could be the same). Thus, long watches proved to be greatly imprecise, and applicable only when a number of very specific

conditions apply. This method is generally not recommended unless all other options are not possible. Finally counts were carried out along two habitual flyways used daily by Grey Parrots to go to roost on Príncipe. Daily and seasonal variability in the number of birds flying by, as well as the relationship with the total population of the island estimated with distance sampling, were examined in order to understand if and how flyway counts can be used to monitor parrot populations. While highlighting the advantages and limitations of all the tested methods, a hierarchical approach to surveying parrot species is proposed in order to employ in each situation the most accurate and precise method proportionately at the local resources and logistics.

3.2. Introduction

Estimates of population size, and trends in abundance, are essential for the development and coherence of conservation and management plans for any wild animal species (Primack 1993, Newson et al. 2008), and they form the cornerstones of the IUCN Red List scheme (IUCN 2014). In species which are harvested from the wild and traded internationally, population monitoring becomes a legal requirement imposed by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 2015). However, with such high numbers of threatened species and limited resources available (James et al. 1999), there is a need for practical, rapid and inexpensive methods to provide reliable metrics of animal abundance (Lancia et al. 1994, Carbone et al. 2001). Parrots are among the world's most threatened groups of birds, owing to habitat alteration and direct exploitation for the pet trade (Collar and Juniper 1992, Snyder et al. 2000), and they are also particularly difficult to survey accurately (Casagrande and Beissinger 1997). They are usually infrequent (Snyder et al. 2000), occur in complex habitats such as tall rainforest (Lee and Marsden 2012), cryptic at rest, social in nature, and are capable of long flights between feeding and roosting sites (e.g. Dändliker 1992a; Juniper & Parr, 2003). As a result density estimates are available only for 25% of the world parrot species, regardless of their conservation status or biogeographical region (Marsden and Royle 2015).

Several methods have been proposed for parrot abundance estimation, ranging from direct counts of species with very restricted ranges, roost counts (Pithon and Dytham 1999, Cougill and Marsden 2004), encounter rates (Thiollay 1992, Holbech 2005), mark-resighting (Casagrande and Beissinger 1997) and distance sampling either from points (Marsden, 1999) or transects (Lee and Marsden 2012). Distance sampling has dominated efforts in the last twenty years (Casagrande and Beissinger 1997, Thomas et al. 2010), and more than 80% of parrot population estimates have been derived using these methods (Marsden and Royle 2015). Distance sampling surveys give ecologists the opportunity to account for site-specific detectability, and for those factors which may affect it (e.g. habitat, time of day, weather conditions, observer, bird behaviour), through the inclusion of covariates in the analysis of the data (i.e. multiple-covariate distance sampling; (Marques and Buckland 2003, Marques et al. 2007). However, distance sampling is time-consuming and resource-demanding, and requires a large number of perched encounters to allow precise density estimation (Buckland et al. 1993). Such sample sizes, in the order of 50–80 records, are practically impossible for rare species (Buckland et al. 2008). Moreover, accurate estimates rely on skilled surveyors who can ensure than none of the assumptions on which the method hinges is violated (Thomas et al. 2010).

In a world where economic resources are always limited, and surveying skills patchily available, there is promise in the development of alternative inexpensive methods to estimate animal densities (Lancia et al. 1994, Carbone et al. 2001). Parrot conservation in particular would benefit greatly from an easy method capable of inferring densities for both rare and common species in a variety of habitats where difficult access and low budgets make more technically sophisticated methods unfeasible. Parrot densities and populations are particularly difficult to estimate owing to their peculiar characteristics. They are extremely mobile canopy-dwelling birds capable of flying long distances in large flocks composed of several species (Chapman et al. 1989), and they often inhabit dense forests where poor visibility, their cryptic coloration and secretive behaviour inhibit detection when they perch (Collar 1998).

Three simple methods which have been used for parrots in the past are: simple encounter rates (e.g. Pizo et al. 1997) , canopy-based surveys or long watches (e.g. Bjork 2004), and counting along flyways (e.g. Amuno et al. 2007). Encounter rates have long been used as means of monitoring population trends (Boitani and Fuller 2000), although a growing body of evidence has highlighted its potential and utility as a proxy of actual population densities (Carbone et al. 2001, Plumptre and Cox 2006, Craigie et al. 2010). Canopy-based surveys have been employed mainly in studies of raptors in tropical forests (Thiollay 1989, Whitacre et al. 1991), but they have also been used to investigate a number of other canopy-dwelling species (e.g. parrots and hornbills; Kemp et al. 2011) . In most cases, results from these surveys have been used only as indices of relative abundance (Gilardi and Munn 1998, Naka and Stouffer 2004), but at times they have also been utilized to infer on actual abundances (Bjork 2004, Kemp et al. 2011), although their accuracy may be questionable owing to detectability limitations intrinsic to the method. Finally, flyway counts have been extensively employed to quantify and monitor raptor migration passage (Therrien et al. 2012, Jaffré et al. 2013), while their use for estimating parrot abundance has been relatively limited (Amuno et al. 2007, Mzumara 2014). Despite the extensive use of some of these methods, their accuracy and precision in estimating parrot abundance have never been validated on robust empirical grounds.

The aim of this chapter is to explore the efficacy of three relatively simple methods to assess abundance and abundance change in parrots, using grey parrots *Psittacus* spp. as model species. Specifically, the objectives are:

1. To examine the relationship between a simple encounter rate (number of birds or groups per hour), derived from casual walks and stops in the forest, and population density estimates derived for grey parrots at the same sites, across Africa, using line transect distance sampling.

2. To determine if there is a relationship between local density estimates for Grey Parrots *P. erithacus* on Príncipe and the number of parrots recorded during long watches from vantage points overlooking forest in the same areas.

3. To explore the efficacy of using counts of birds as they move along flyways on Príncipe as a method of long-term monitoring of relative parrot numbers by relating counts to density estimates and investigating diurnal variability in flights patterns and volume, and other confounding factors.

3.3. Methods

3.3.1. Study species

The grey parrots *Psittacus* spp., now classified as two species (del Hoyo and Collar 2014), Grey Parrot *P. erithacus* (Central Africa to eastern Côte d'Ivoire; Figure 1) and Timneh Parrot *P. timneh* (western Côte d'Ivoire to Guinea-Bissau), have a long history of heavy exploitation for national and international trade capture (UNEP-WCMC 2014), and there is grave concern that harvest levels involved are unsustainable (CITES 2006). Both species have been now uplisted to IUCN status 'Vulnerable' because of severe declines and local extinctions, making population estimation and monitoring a conservation priority (BirdLife International 2014). The two species have a vast range, extending over three million km^2 across Central and West Africa (BirdLife International 2014). Both species rely largely on forested areas, and have presumably been impacted by forest loss and degradation, especially in West Africa (Vittek et al. 2014). Their large ranges, forest habitat, and patchy distribution present problems of sampling at a sufficient number of sites to produce reliable overall estimates. Despite several attempts, efforts to survey the species accurately have hitherto been hampered by methodological issues, lack of expertise, and simply the enormity of the task.

3.3.2. Line transect distance sampling

Line transect distance sampling (LTDS) is a well-established survey method for a range of taxa, including parrots (Casagrande and Beissinger 1997, Marsden and Royle 2015). It involves walking transects of known length and recording, for each encounter, the perpendicular distance from the bird/s to the transect line. Records from various transects are pooled together and (usually) the program DISTANCE is

used to model the fall-off in detectability with increasing distance from the transect line (Thomas et al. 2010). Important assumptions are: that transects are positioned randomly in respect to the bird population; that birds do not move (naturally or in response to the observer) during the counting process; that distances to objects are known without error (or with small and random error); and, most importantly, that probability of detecting animals on the transect line is certain (Buckland et al. 2005). This last assumption can be relaxed in some surveys, for example if the probability of detection at zero metres g(0), is not measured, but realistically presumed, or in double-observer distance sampling (e.g. Buckland et al. 2010). Owing to its reliability and precision we used LTDS as a gauge to test all three of our objectives.

Parrots were counted along transects which were around 2–6 km long, walked at speeds of 1–1.5 km per hour between 06:30 and 11:00 h, in the absence of rain or strong wind that might affect bird detectability (Lee and Marsden 2012). Parrots were detected by both sight and sound, and their perpendicular distance at first detection recorded. Only records of perched parrots were included in the analysis as inclusion of flying birds seriously inflates estimates (Marsden 1999). Surveys were conducted at very similar times of year at all sites, corresponding to the non-breeding season in Liberia and other West African countries, including Príncipe, and possibly the onset of breeding in Central Africa (Benson et al. 1988).

DISTANCE 6.2 (Thomas et al. 2010) software was used to calculate parrot density at each site (individuals km^{-2}). Multiple-covariates distance sampling (MCDS) engine was used, performed with a half-normal key function with cosine adjustment term. 'Site' was included in the analysis as a covariate (Marques et al. 2007) to go some way towards addressing detectability differences across sites. The best model was selected using Akaike's Information Criterion (AIC; Akaike 1974) minimisation. Parrot sightings were entered as clusters (number of birds in each group) with exact distances rather than in distance bands. The furthest 5% of distance records were removed (right-hand truncated).

3.3.3. Objective 1

Study area

Data in support of Objective 1 were collected from ten sites in five countries in West and Central Africa (Figure 1; Table 1) as part of a CITES/BirdLife International project (in which SV participated) on strengthening trade management for the species (CITES 2013). Fieldwork was centred on areas that local BirdLife partners knew or were suspected still to hold reasonable parrot numbers. These were usually within or adjacent to protected areas. Exceptions were some fieldwork in agricultural areas with remnant forest patches around Yaoundé, in Cameroon, and surveys on Príncipe, which is largely unprotected but which has extensive forest and high numbers of parrots. Two protected areas in Cameroon (Lobéké and Campo Ma'an National Parks) were subdivided into two geographical zones.
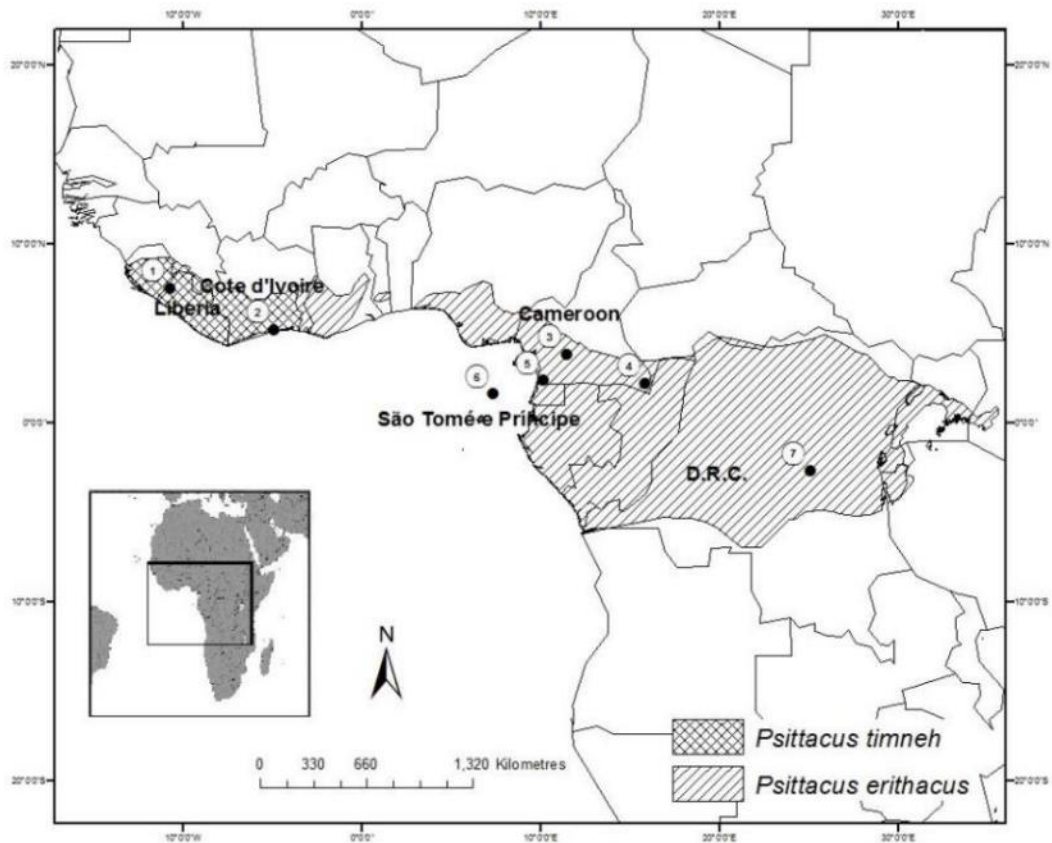
Figure3.1. **Map of West and Central Africa showing the ranges of Grey and Timneh Parrots and the survey sites numbered as follows: 1. Gola Forest (Across the River Transboundary Peace Park), Liberia; 2. Various sites Cote d'Ivoire; 3. Agricultural sites around Yaoundé, Cameroon; 4. Lobéké National Park, Cameroon; 5. Campo Ma'an National Park, Cameroon; 6. North and South Príncipe; 7. TL2, Democratic Republic of Congo.**

Table 3.31. Details of the study sites and parrot surveys. Total km surveyed and number of transects includes line transect distance sampling only.

Country	Site	Coordinates	Habitats	Dates	Tot.km	No. of transects
Cameroon	Lobéké National Park (East; Djembe)	2°11'38"N 16°04'07"E	Logged forest (> 15 years previously)	7/7-10/7/13	20.0	5
	Lobéké National Park (West; Djangui)	2°17'19"N 15°38'44"E	Logged (> 15 years) and primary forest	10/7-13/7/13	17.5	4
	Campo Ma'an National Park (South)	2°15'36"N 9°59'59"E	Logged (> 10 years) and primary forest	13/8-16/8/13	23.5	6
	Campo Ma'an National Park (North)	2°27'58"N 10°22'26"E	Logged (> 10 years) and primary forest	17/8-20/8/13	18.5	4
	Agricultural land outside Yaoundé	3°50'21"N 11°30'21"E	Agroforestry and secondary forest	3/7-19/7/13	11.3	3
Côte d'Ivoire	Parc National du Banco; Réserve Dahlia fleur; Parc National d'Azagny; Zone rurale de Soubré	5°12'45"N 4°52'24"W	Primary/secondary forest; agroforest	7/8-19/8	32	7
D. R. Congo	TL2 (Tshuapa–Lomami–Lualaba Conservation Landscape)	2°41'12"S 25°08'15"E	Primary forest on white sand	16/8-26/8/13	108.4	7
São Tomé e Príncipe	Príncipe North	1°39'33"N 7°23'41"E	Secondary forest; agroforest	16/6-22/8/12	9.9	7
	Príncipe South	1°34'33.91"N 7°22'32.80"E	Primary and secondary forest	16/6-22/8/12	9.8	7
Liberia	Gola forest (Across the River Transboundary Peace Park)	7°32'07"N 10°42'60"W	Secondary and logged forest; agroforest	8/8–29/9/13	42.7	9

Experimental design

At all sites, distance sampling line transects and simple encounter rate surveys were conducted in the same areas. Some transects were walked using both methods, others not. Transects were chosen to cover the site as wholly as possible and to be representative of the habitats at the site. Transects were not cut especially for the study due to time constraints, but were positioned along existing tracks such as ranger trails and overgrown logging skid trails. Transects were walked only once for each method. No transect was walked using both methods on the same day, except for transects at one of the ten sites, TL2 in D. R. Congo, where data from the same transects were used to calculate both density estimates and encounter rates. Parrots were counted by one to three teams of recorders. Surveys were done at similar times of year by different surveyors, i.e. Cameroon 4 July to 19 August 2013, Príncipe 16 June to 22 August 2012; D.R. Congo 8 to 29 August 2013; Côte d'Ivoire 2 to 29 August 2013 and Liberia 8 August to 28 September 2013. All recorders were trained and briefed in distance sampling and encounter rate methods prior to the surveys, and all surveys had at least one fieldworker with months of experience with distance sampling (except Côte d'Ivoire, where no grey parrots were actually recorded). Inclusion of 'Site' as a covariate in DISTANCE (see later) went some way towards accounting for any differences in detection patterns across recorders.

Encounter rates

Encounter rates (ERs) have a long history in conservation ecology but have become less often used recently owing to bias associated with differences in detectability across species and habitats, and the need for actual population estimates rather than abundance indices (e.g. Buckland et al. 2008) . They involve walking, standing or other detection methods, and counting animals/groups per hour of recording, unit of distance walked, or mist-net capture effort expended (Lancia et al. 1994).

Encounter rate data (number of groups/individuals per hour of searching) were collected by the same teams as those doing distance sampling, and in the same areas. Transects which were walked one day using LTDS were surveyed using ER on a different day, usually within two days and at most five days. Path width could be greater with ER than with LTDS, and some ER surveys were carried out along roads. ER sampling was done between 06:30 and 12:00 h and 16:00 to 18:30 h. This survey period was less constrained than that used for LTDS. Several authors have stressed the importance of restricting distance sampling surveys to those periods when birds are most detectable, and hence probability of detection close to the transect line (distance = 0 m) is most likely to be certain (e.g. Bibby et al. 2012) . The survey period for ER surveys was extended to the late afternoon, both to boost sample sizes and to reflect better how ER methods might be used in future parrot surveys.

Recorders could spend variable amounts of time walking or standing, and, after each half-hour period, they recorded whether they were standing still or walking, took a GPS reading and made a broad habitat type assessment (primary forest, secondary forest, agroforest, logged forest, agriculture land). Importantly, while records of flying parrots were excluded from LTDS surveys (see above), they were included in ER calculations. There were two reasons for this. First, the intention was to test whether the ER method might be a useful surrogate for LTDS in areas of low parrot density; hence inclusion of aerial parrots was seen as appropriate to maximise sample sizes, especially in areas where parrots are rare. Second, surrogate ER methods might, in the future, be undertaken by those not trained in parrot survey methods. It can be difficult to determine whether parrots (especially those heard only or heard first) are in flight or whether they were flushed or even perched. Proportions of parrot individuals recorded on surveys which are in flight are generally high (Marsden 1999).

The relationship between parrot density and encounter rates

LTDS and ER data from 10 sites were accumulated (Table 1). Spearman's rank correlations were used to examine the relationship between density estimates using MCDS and encounter rates (groups and individuals), and mean group size across the ten sites. A Reduced/Ranged Major Axis (RMA) regression (Ryan 2008) was then used to examine the relationship further. This method is appropriate when both the dependent variable and predictor included errors (Legendre and Legendre 1998). An intercept was included in the model because ER was not assumed to be zero when density is zero, since parrots can be recorded flying over areas where their 'on-the-ground' density is zero. All analyses were performed in R (R Core Team 2014): the package 'lmodel2' was used for the RMA regression and the package 'ggplo2' for plotting the correlation with a 95% prediction interval.

3.3.4. Objective 2

Study area and experimental design

To address Objective 2, nine elevated vantage points on Príncipe were selected to conduct 'long watch' censuses (Fig. 2). These offered a wide and unobstructed view over a portion of forest of variable size, and from which parrots could be easily seen or heard. Neither random nor systematic selection was possible, as few sites in the study area fitted requirements in terms of visibility. The island of Príncipe was divided into in 133 1-km^2 square sample plots based on the Universal Transverse Mercator (UTM) projection. Each vantage point looked out on one or two different square sample plots where Line Transect Distance Sampling (LTDS) surveys were performed. All nine areas were surveyed using both methods, once after the fledging period (March–April 2014) and again just before the following breeding season (August–September 2014). LTDS and long watches were never performed more than 30 days apart and, for the sake of data independence, were never carried out on the same day. Where the long watches looked over more than one square sample plot, the mean density was weighted by the proportion of area which fell in each square. Different lookouts might look on adjacent squares but never on the

same one. For logistic reasons, all vantage points were located in the north of the island, since the south is difficult of access and covered by untouched primary forest. For each vantage point geographic coordinates and elevation were recorded with a GPS, while the width of the field of view was measured with a compass. Maximum distance of detection (MDD, i.e. maximum distance to which Grey Parrots could be both seen and heard and beyond which they were not counted) was quantified by identifying clearly recognisable natural landmarks. A calculation of surveyed (i.e. visible) areas was carried out by using a combination of cartographic techniques and satellite imagery, and area surface was calculated by using Google Earth Pro (Google Inc.).
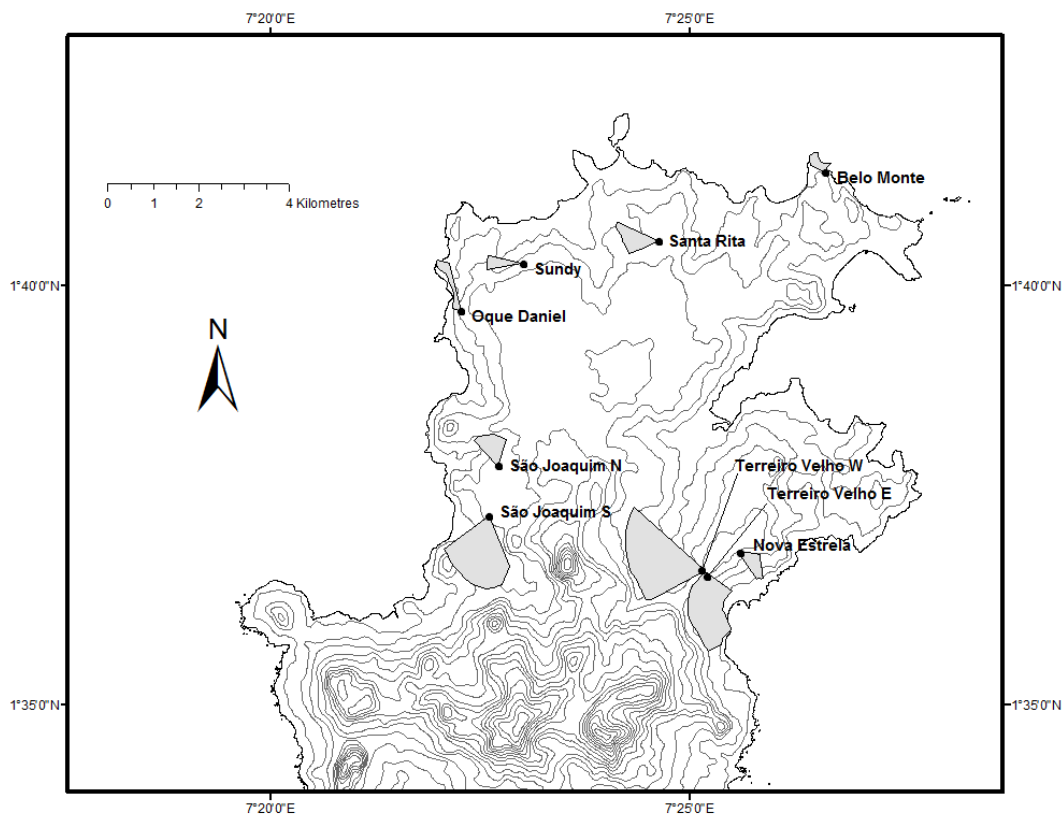
Figure 3.2. Detail of the north of Príncipe with the location of the nine vantage points (dots) from which the long watches were carried out and the respective areas surveyed (grey).

Long watches

One observer counted all Grey Parrots seen flying in, out of and over the underlying area during four different three-hour time slots (i.e. early morning 06:00–09:00, late morning 09:00–12:00, early afternoon 12:00–15:00, late afternoon 15:00–17:45), each one on a different day, in order to account for variations in detectability at different times owing to differences in parrots activity. All observations were performed by the same surveyor, who never counted in more than two observation periods per day or two observations in a row, in order to avoid a decline in detection due to observer weariness (Gregory et al. 2004). Counts were carried out only in good visibility and were suspended if weather conditions deteriorated.

The relationship between parrot density and long watches

Wilcoxon signed-rank test was employed to test independence of data collected from the same site but for different seasons. A Kruskal-Wallis test was performed to test variability in bird encounters between the four different time slots. For the sake of the successive analyses, data from the second and third time-slots were lumped together since these two were the periods with least encounters and were possibly least affected by the occasional passage of birds from other areas. Linear mixed effects models were used to explore possible relationships between mean parrot densities and the number of outbound and total flights, including the variable 'Site' as a random factor to account for the possible effects of pseudoreplication. The same statistical tests were then performed after having excluded the three largest areas from the dataset, since the smallest among these was significantly bigger (i.e. 400%) than the rest, which in turn may have affected detectability.

3.3.5. Objective 3

Flyway counts

This protocol was based on the surveys previously developed and implemented by Melo (2003). Grey Parrots in Príncipe move regularly between feeding areas in the north and roosting sites in the south of the island. These movements occur at the

rising and setting of the sun, but the latter offers the better conditions for parrot counts. Counts were conducted from two distinct points, i.e. Bela Vista (1°37'04" N - 7°24'49" E) and São Joaquim (1°37'16" N - 7°22'38" E). These two points offer clear views of the preferred flyways used by the parrots to return to their roost sites. Counts were previously performed once at each site in April 2003 (Melo 2003) and were repeated during the PhD study in 2012 (five times in each site in August) and in 2014 both in the post-breeding (five times in each site in March–April) and pre-breeding (three times in each site in September–October) seasons. Similarly structured counts were carried out in 1997 and 1998 in two different sites (i.e. Terreiro Velho and Ponta do Sol) and it has been suggested they offered similar visibility to the Bela Vista and São Joaquim flyways respectively (Melo 2003). Nonetheless, owing to their questionable comparability, the data from these earlier surveys were not used for further analyses, but are reported in table 4 for sake of completeness. Counts were carried out by two observers strategically positioned in order to control the largest possible area. Each observer would be in charge of counting parrots flying over a section equal to half of the total area. Groups which flew over the border between the two sections (i.e. hard to attribute to either) were recorded separately by both counters with the exact time of passage. These records were then sorted later in order to avoid double-counting. The area was divided equally between the two observers. Observers were ready by 16:00 (i.e. 3 hours before sunset) and counts continued while visibility allowed (up to ca. 17:45). Days when the counts had been interrupted due to bad weather were repeated. Time of passage, group size, and direction of flight (i.e. southbound to the roosting areas or northbound to the feeding areas) were recorded for each group flying by during the survey period. Southbound parrots were subtracted from the number of northbound individuals to account for possible double counts and quantify the net flow of southbound birds. Wilcoxon signed-rank and Kruskal-Wallis tests were used to explore the possible differences in the number of birds flying over, the proportion of birds flying against the predominant direction of flight and the mean group sizes between the different flyways, seasons and counts. Where available (i.e. 2003 and 2014 in pre- and post-breeding seasons), the ratio (%) of the flyway count results to

the LTDS results was calculated for each site and for the whole island in an attempt to define a relationship between results from the two methods.

3.4. Results

3.4.1. Abundance estimates across grey parrots' range

Table 2 shows the great variability in density estimates and encounter rates across the ten sites. In Côte d'Ivoire, no parrots were recorded along either LTDS or ER transects (32 km and 85 h respectively), and density estimates and encounter rates from D. R. Congo were very low (0.42 ± 0.29 individuals km^{-2} and 0.08 ± 0.02 parrot groups h^{-1}). The highest densities were estimated in Príncipe North (76.8 ± 22.2 individuals km^{-2}), with an ER of 6.0 ± 1.8 parrot groups h^{-1}. Densities in Cameroon's protected areas were high, especially at Lobéké National Park, which had the highest density estimate of any mainland Africa site (29.6 ± 7.7 individuals km^{-2}). Overall mean group size was 1.98 ± 0.34, with the largest flock recorded being of 20 individuals at Lobéké East.

Table 3.42. Population density estimates (birds km^{-2}), encounter rates (groups h^{-1} and individuals h^{-1}), and mean group sizes (all ± standard error) from the ten survey sites. Density estimates were calculated those using Multiple Covariates Distance Sampling (MCDS) with 'Site' as a covariate. Also included are overall population density estimates for Campo Ma'an and Lobéké National Parks, and the island of Príncipe.

Site	Country	Density estimate (MCDS)	Encounter rate (groups)	Encounter rate (individuals)	Mean group size
Campo Ma'an South	Cameroon	14.7 ± 4.9	0.79 ± 0.33	2.05 ± 0.5	4.2 ± 2.0
Campo Ma'an North	Cameroon	7.5 ± 2.5	1.8 ± 0.39	5.39 ± 1.59	2.7 ± 0.49
Campo Ma'an NP	Cameroon	10.9 ± 2.9			
Agricultural land near Yaoundé	Cameroon	4.1 ± 2.9	1.0	2.5	2.5
Lobéké East	Cameroon	40.3 ± 13.2	2.65 ± 0.59	6.77 ± 2.69	2.2 ± 0.41
Lobéké West	Cameroon	21.0 ± 6.9	2.23 ± 0.25	3.94 ± 0.56	1.8 ±0.18
Lobéké NP	Cameroon	29.6 ± 7.7			
Côte d'Ivoire	Côte d'Ivoire	0	0	0	0
Gola forest	Liberia	2.2 ± 1.1	0.26 ± 0.13	0.48 ± 0.19	1.7 ± 0.51
Príncipe North	São Tomé e Príncipe	76.8 ± 22.2	6.04 ± 1.84	14.3 ± 5.7	1.8 ± 0.42
Príncipe South	São Tomé e Príncipe	35.1 ± 14.4	5.58 ± 1.97	13.3 ± 6.4	1.5 ± 0.46
Príncipe island	São Tomé e Príncipe	53.0 ± 13.1			
TL2	DRC	0.42 ± 0.29	0.08 ± 0.02	0.16 ± 0.06	1.52 ± 0.4

3.4.2. The density-encounter rate relationship

There was a strong relationship between estimated density and encounter rates of groups (r_s = +0.95, n = 10, p < 0.001; Figure 2). Encounter rates of groups h^{-1} were strongly correlated with ERs of numbers of individual birds h^{-1} (r_s = +0.93, n = 10, p <

0.01), but there was no relationship between density estimates and mean parrot group sizes (r_s = +0.29, n = 10, p = 0.40). The reduced major axis (RMA) regression (R^2 = 0.80, df = 9, p = 0.01) had the equation: Encounter rate = (0.088 * Density) + 0.22.
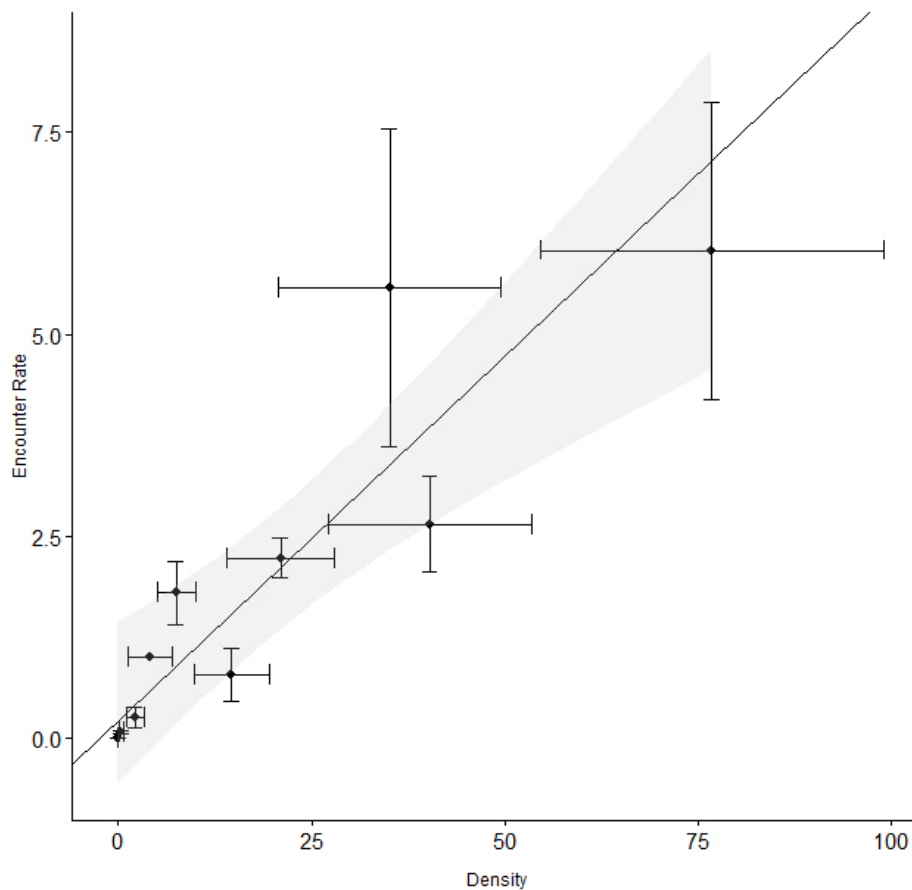
Figure 3.3. The relationship between parrot density estimates (birds km^{-2} ± SE), and encounter rates (groups recorded per hour ± SE), with 95% prediction region (shaded).

3.4.3. The relationship between local densities and long watches

There was no significant difference in the density estimates (form LTDS) in individual squares between the two seasons; thus independence of data from the same sites was not confirmed (W = 640, p = 0.93). The number of outbound and total flights recorded for each area was significantly different between time slots (H = 26.71, p < 0.001; H = 25.14, p < 0.001 respectively, Fig.4).
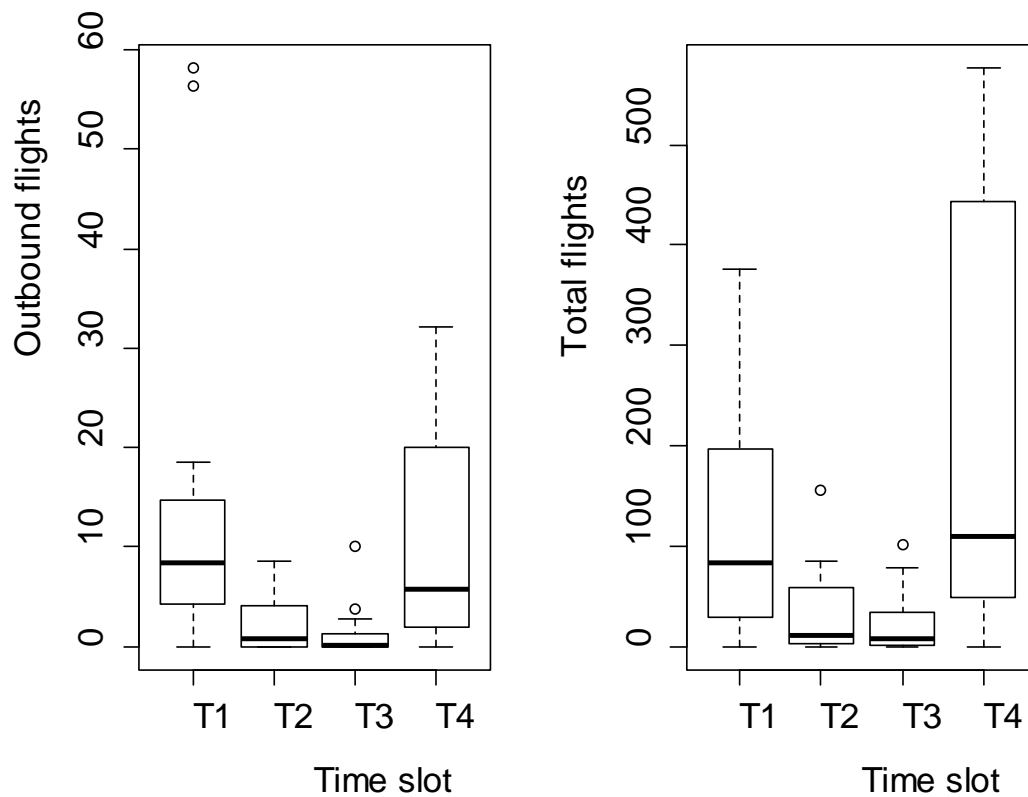
Figure 3.4. Difference in number of outbound and total flights recorded for each area among time slots.

There was a significant correlation between mean densities and the number of outbound flights recorded (LME model, F = 14.06, df = 5, p < 0.05, Fig. 5) for observations made in the last three hours of the day. No relationship was found between mean densities and the outbound or total flights, in all the other time-slots. (Table 3).

Table 3.43. Results of linear mixed effect models exploring the relationship between outbound or total flights and mean density for the different time-slots, with 'Site' as a random factor. Here reported are intercept (α), slope (β), F- and p-values for each model.

	T1			
	α	β	F	p
Outbound	2.44	0.03	3.02	0.14
Total	10.64	0.02	0.21	0.67
	T2			
Outbound	–	–	–	–
Total	2.88	0.04	2.69	0.12
	T3			
Outbound	2.29	0.02	14.06	0.01*
Total	14.04	0.03	0.79	0.41

*= 0.05 significance level
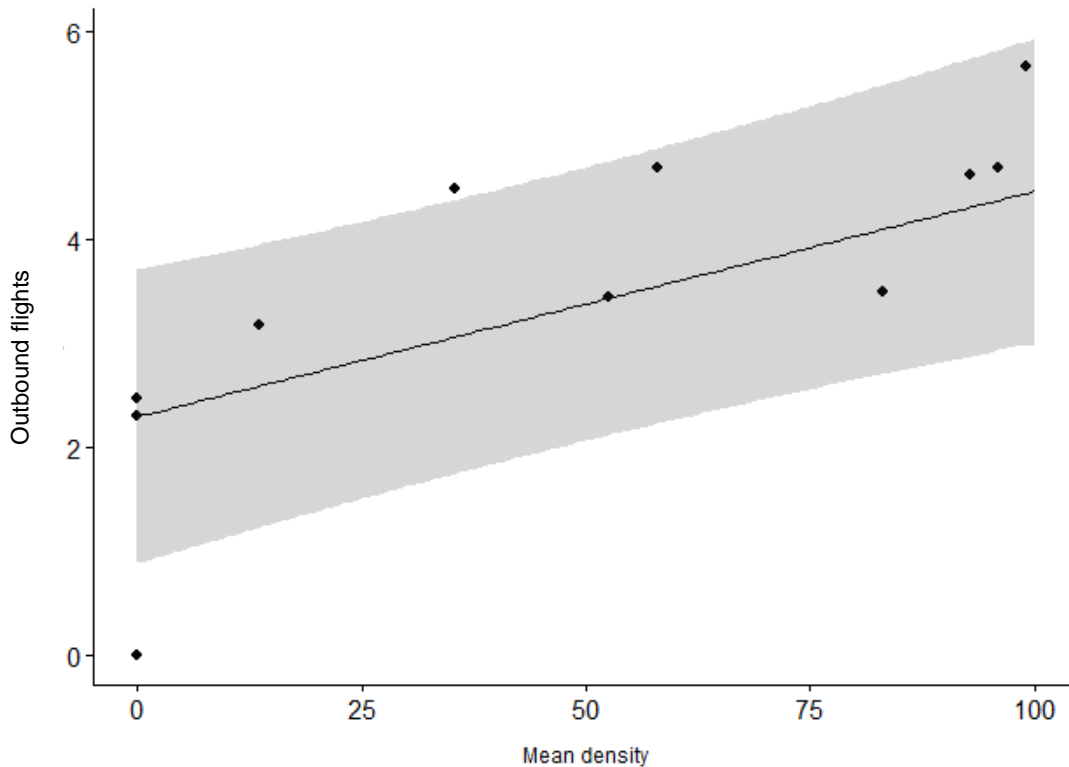
Figure 3.5. Relationship between the mean density (birds km^{-2} ± SE) and the number outbound flights (square root transformed), with 95% prediction region (shaded).

3.4.4. Variability of flyway count results

Counts produced a mean (± SD) of 597 ± 200 bird encounters in Bela Vista and 1,059 ± 145 SD for São Joaquim. Of these, most parrots followed the same main southbound flight direction (i.e. to the roosting sites), although a proportion of birds were recorded flying in the opposite direction (mean % ± SD: 9.2 ± 7.4 in Bela Vista and 4.6 ± 4.0 in São Joaquim). These proportions did not differ significantly between flyways ($W = 121$, $p = 0.06$), but did differ between pre- and post-breeding period ($W = 154$, $p < 0.01$), and between counts ($H = 17.37$, $p < 0.001$, Fig. 7).
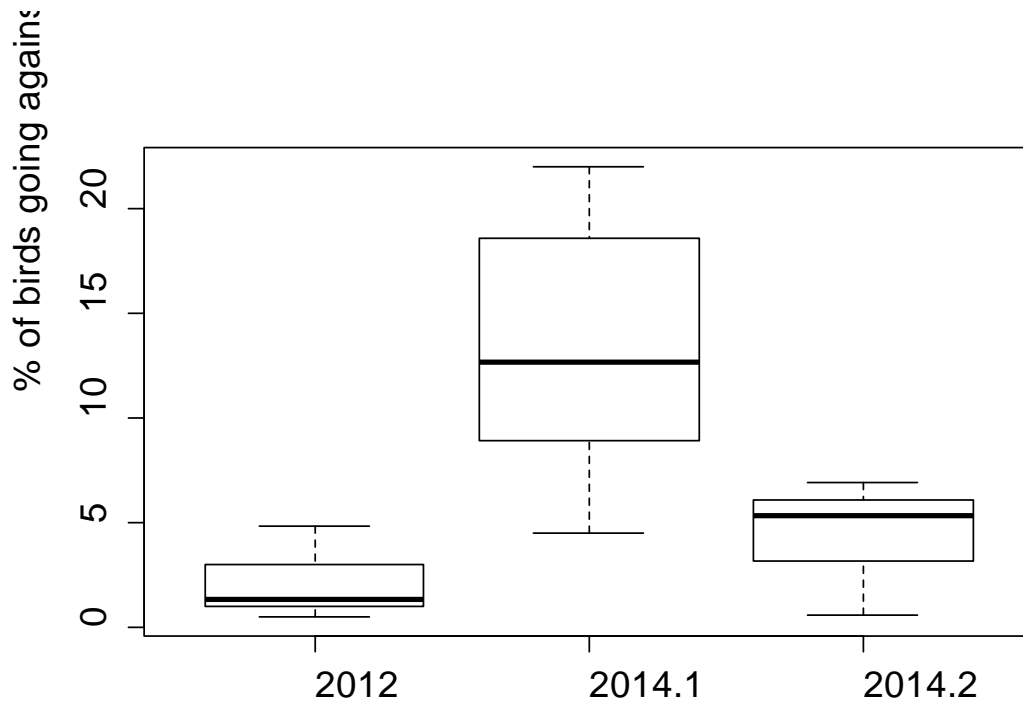
Figure 3.6. Difference in the proportion (%) of birds flying against the main southbound direction, among the 2012, 2014 pre-breeding (2014.1) and 2014 post-breeding (2014.2) counts.

The mean (± SD) number of flyover southbound parrots at Bela Vista (462 ± 80) was significantly lower than that (955 ± 91) passing São Joaquim ($W = 0$, $p < 0.001$), but not between pre- and post-breeding seasons ($W = 97$, $p = 0.38$). Counts in Bela Vista averaged 0.58 ± 0.19 (SD) times the counts from São Joaquim.

Finally the mean group size was significantly different between pre- and post-breeding seasons ($W = 16.5$, $p < 0.001$. Fig.7) and between counts ($H = 16.45$, $p < 0.001$), but not between flyways ($W = 83$, $p = 0.96$).
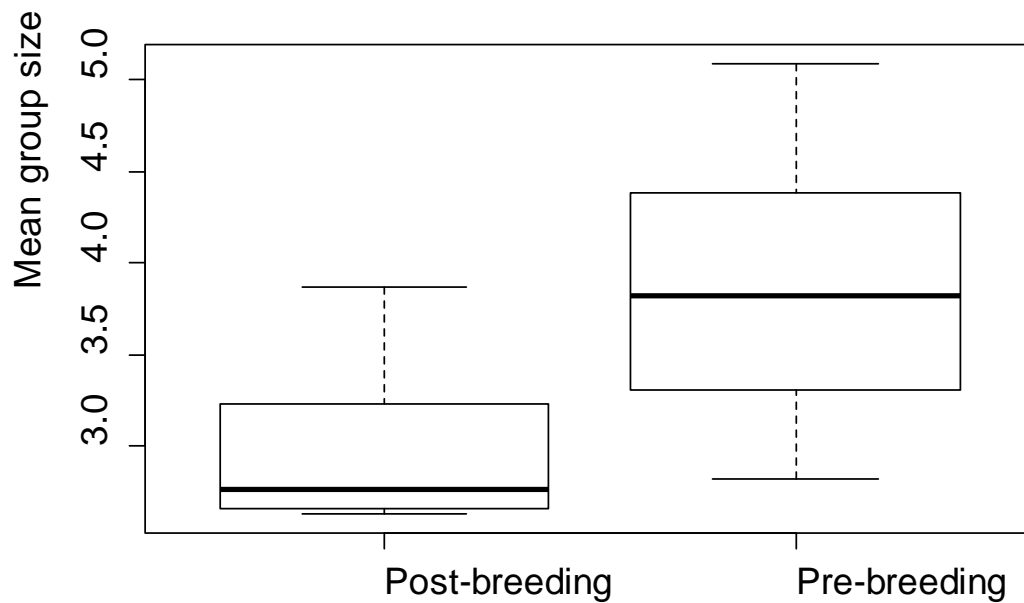
Figure 3.7. Difference in the mean group size between pre-and post-breeding seasons.

Table 4 reports the results from all counts. The mean percentage (± SD) ratio of flyway count results to LTDS results is 0.06 ± 0.01 for Bela Vista, 0.13 ± 0.02 for São Joaquim and 0.19 ± 0.03 overall.

Table 3.44. Results from flyway counts performed in 1997 (mean ± SD and min-max range from 13 repeats in Bela Vista and 11 in São Joaquim), 1998 (totals only as daily data not available), 2003 (totals from one repeat each site), 2012 (mean ± SD and min-max range from five repeats each site), 2014 in pre-breeding season (mean ± SD and min-max range from five repeats each site) and 2014 in post-breeding season (mean ± SD and min-max range from three repeats each site). Grey Parrot total population estimate (± SE) in Príncipe obtained by LTDS is reported where available. Finally the percentage ratio of the total results for the island and for each site for the two methods is given.

	1997 Pre-breeding	1998 Pre-breeding	_	2003 Post-breeding	_	2012 Pre-breeding	_	2014 Pre-breeding	2014 Post-breeding
Bela Vista	460 ± 58 (363-535)	399	–	235	–	410 ± 82 (299-508)	–	505 ± 51 (496-540)	477 ± 92 (408-582)
São Joaquim	240 ± 84 (105-350)	309	–	273	–	936 ± 53 (868-1,012)	–	970 ± 109 (858-1,076)	948 ± 171 (786-1,127)
Total	700	708	–	508	–	1,345	–	1,475	1,425
LTDS	–	–	–	–	–	8,388 ± 741	–	7,996 ± 568	6,517 ± 361
$\frac{Total}{LTDS}$ %	–	–	–	–	–	0.16	–	0.18	0.22
$\frac{Bela\ Vista}{LTDS}$ %	–	–	–	–	–	0.05	–	0.06	0.07
$\frac{São\ Joaquim}{LTDS}$ %	–	–	–	–	–	0.11	–	0.12	0.14

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3.5. Discussion

Ideally, abundance estimates for conservation-important species should derive from high-quality data collected during standardised surveys (Sutherland 2006). Such surveys should accumulate large numbers of records to allow precise density estimation (Marsden 1999), and should account for differences in detectability across sites and species (Buckland et al. 2005). Distance sampling is the method of choice for many tropical birds in general, and parrots in particular (Marsden and Royle 2015), since it allows, if suitably designed, to take into account a range of uncontrollable variables that may affect detectability and, in turn, precision and accuracy of the estimate (Marques et al. 2007). Although ideal, in many parts of the world distance sampling methods are not an option as the expertise needed to design and execute the surveys and to analyse the resulting data is missing. Moreover, the lack of economic resources often means that it is impossible to fund extensive and/or repeated surveys, and to overcome the logistical difficulties of surveying parrots in large and remote areas. Hence the need exists for simple and inexpensive methods to estimate parrot densities in order promptly to inform conservation practitioners in their decisions.

3.5.1. Encounter rates as surrogates for density estimates?

The demonstrated relationship between estimated density and encounter rate means that the latter may be used as a surrogate for the former with reasonable confidence. Of course, there are a number of issues producing noise in the relationship between the two measures. Sites may have different parrot detectability (Buckland et al. 2005), observers possess different abilities to detect birds, especially at larger distances, parrots might fly more often at some sites than others (Marsden 1999), and parrot group sizes may differ across sites and seasons (if birds are in larger groups then fewer groups may be encountered for a given population density). Nevertheless, as has been found in other situations (e.g. Danielsen et al. 2005), an encounter rate method can be a useful tool – in this case for assessing grey parrot abundance in situations where economic resources and/or distance sampling skills

are lacking. Of course, these calibrations apply only to grey parrots, and, if deemed appropriate in other species, then species- and situation-specific calibrations would need to be made to support the relationship between the more technically sophisticated survey method and the simpler surrogate.

Under-predicting density using this surrogate method is not as great a problem, in conservation terms, as mistakenly predicting high density, when density is in fact low. The 95% prediction region in Figure 3 shows the degree of uncertainty that might arise from short parrot surveys. Intervals are wide when abundance is high but this is probably not a great problem as these are the population levels at which distance sampling would be most feasible. Note that an encounter rate of over one parrot group per hour, a rate far and above what would be recorded over much of the species' range, can still be associated with an effective population density of zero. This is because records of flying birds are included in the encounter rate method, but not the density estimates. In effect, density within the sampled area is zero, but parrots are still recorded flying over the sampled site.

Importantly, the method will allow us to gauge abundance in situations where parrots are far too rare to be effectively surveyed using distance sampling. The regression indicated that an average encounter rate of one flying or perched group per hour in forest habitat corresponded to a density estimate of around 10–15 birds km^{-2}. At such densities, it is likely that line transect distance sampling will be feasible, but it is in the many areas, especially in West Africa, where parrot densities are very much lower, that the value of encounter rate calibration lies. One parrot group per (ten-hour) day corresponds to a density of around one bird km^{-2}, thus some protected areas in Nigeria or Ghana where bird tours and visiting ecologists encountered one group per 5–7 days of survey (Olmos & Turshak 2009, F. Dowsett-Lemaire *in litt.* to BirdLife's Globally Threatened Bird Forums, 27 January 2012) almost certainly hold negligible local parrot densities. The relationship represents a key link between quantitative and anecdotal data, which could be of use in areas where the latter is the only information available. Opportunistic observations collected by forest guards, birdwatchers or scientists studying other groups could easily be converted into encounter rates and thus provide first 'ball-park' indications of likely population

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density for many areas. Where appropriate and feasible, the same technique could be used with historical data, to build estimates of former abundances and thus serve as a yardstick to measure population trends. The lack of quantitative historic data on the abundance of grey parrots in many parts of their ranges has probably hampered efforts to gauge the true extent of declines in the species (Martin et al. 2014).

Carbone et al. (2001) found a relationship between density and rates of camera trap capture for tigers *Panthera tigris* across their range, proposing the latter as a way of inferring the former. The proposal has drawn criticism concerning the precise calibration of the method, and as to whether it would be applicable to other species elsewhere (Jennelle et al. 2002). The method indeed needed refining using independent data collected with a standardised method (Carbone et al. 2002). Moreover, detectability, and therefore encounter rate, can differ greatly among different species and home range sizes, or as a result of different study design (Sollmann et al. 2013). Despite its limitations, however, Carbone et al.'s method has been welcomed by researchers as a useful tool for abundance estimation in a number of species ranging from large carnivores (Linkie et al. 2006) and forest ungulates (Rovero and Marshall 2009) to ground-dwelling birds (Samejima et al. 2012).

 A possible alternative, or complement, to using encounter rates or other proxies for density would be to use Occupancy Modelling (MacKenzie et al. 2002), either as a stand-alone method to detect changes in abundance/occupancy across sites, or as a surrogate for density estimation. Occupancy Modelling uses detection/non-detection data to calculate a detection probability function and to model species occurrence across the study area (MacKenzie 2006). The method is flexible, and relatively quick and easy to perform as compared to distance sampling (Zylstra et al. 2010), so may be well suited to larger areas. The key might be to find the relationship between occupancy values and density estimates, and to use the former in place of encounter rates as a surrogate for the latter. Research on the use of occupancy modelling as a general surrogate for estimates of parrot abundance (Figueira et al. 2015), and especially its value in monitoring populations over time at individual sites such as protected areas (e.g. Burton et al. 2012), may be rewarding.

Results show how variable the abundance of grey parrots is across their ranges. The local availability of food resources, and especially suitable nesting sites, are known to be limiting factors for many parrot populations (Newton 1994, Collar 1997). Although poorly described, competition with other hole-nesting birds might be another factor restricting local abundance (Amuno et al. 2010). Densities from the two Cameroon parks and from Príncipe are much higher than any figure previously presented (see Chapter 2). This is in stark contrast to the near-absence of grey parrots from most of Ghana (Marsden et al. 2013) and their extreme rarity in protected areas in Cote d'Ivoire. In these areas, and indeed across the majority of their ranges, it is difficult to imagine grey parrots being anything other than very rare within, or totally absent from, almost all parts of the landscape in the coming decades.

3.5.2. Do long watches provide accurate evidence of local densities?

The results suggest that flight frequencies as counted from vantage points are not a good representation of local densities as calculated from distance sampling surveys. As such, their used cannot be recommended, although they might provide a broad indication of abundance in very specific conditions and where no other option is available. This is consistent with results from studies on other species of parrots (Symes and Marsden 2007). Long watches present a number of limitations that are difficult to overcome without compromising the original need for a simple and inexpensive method. First, the study area has to be suitable for this type of survey, i.e. it has to present natural elevated vantage points from which the survey can be carried out; if not, the construction of observation towers may be required, significantly increasing the survey budget (e.g. Naka 2004). For example, despite the hilly orography of Príncipe, finding vantage points with an unobstructed view on a sizeable patch forest was challenging. Even if suitable vantage points can be found, it is often problematic to define with any degree of precision the area which can be surveyed, and its overall size is bound to have a significant effect on bird

detectability. Results of this study showed that, if there is any scope in using this method, it is limited to small areas where detectability can be assumed to be more or less the same. Thiollay (1989) highlighted the difficulty of plotting accurately locations of raptors from vantage points as the distance from observer increased. Moreover results from any over-canopy survey are most likely to underestimate density for the quieter, more secretive and less colourful species, especially in steep and densely vegetated areas (Kemp et al. 2011). Finally the long watches need a high number of encounters to be in any way effective, making the method inappropriate for rare or elusive species. The only, albeit weak, relationship found in this study was in last three hours of the day (i.e. the time-slot which had most encounters), although the number of detections then is most likely to be affected by birds travelling through the area to their roosting sites (see § 3.2.8). Interspecific and temporal variability in flight frequency has implications in most bird census techniques (Symes and Marsden 2007). For example, one of the assumptions for the reliability of the distance sampling methods is that birds must be perched when recorded, (Buckland et al. 2008).

Although the long watch method may be suitable for the study of bird species composition (e.g., Naka 2004, Kemp et al. 2011), its use as an index of abundance (e.g. Gilardi and Munn 1998) is questionable if the relationship with actual local abundance has not been tested. Bjork (2004) adjusted the estimates derived from long watches as a function of four variables (sampling site, landscape type, weather conditions, and observer) through the construction of a number of possible statistical models. While this method was not tested empirically, it may also defeat the purpose of finding a simple method implementable with minimal skills. The 95% prediction region of the relationship found between the number of outbound flights and the actual local density (Fig. 5) of Grey Parrots suggests that even in the very few cases where this method may be used (e.g. where the surveyed areas are small enough to ensure similar detectability) this will return only a very broad and imprecise indication of what the abundance may be. Thus, the use of this method is not advisable unless there is no alternative.

3.5.3. Can flyway counts be used to monitor parrot populations?

Flyway counts have been used extensively for estimating migrating raptors (Hoffman and Smith 2003, Jaffré et al. 2013). Nonetheless the use of flyway encounters to estimate populations of resident birds poses a high risk of double-counting. Canopy-dwelling parrots, which inhabit mostly dense tropical forest, are generally highly cryptic birds when perched (Casagrande and Beissinger 1997), but in some areas they seem to use preferential flyways (e.g. rivers) for their regular local movements (e.g. to saltlicks or roosting sites) (Selman et al. 2000, Vaughan et al. 2005). Thus, in these areas, habitual flyways may offer an opportunity for inferring on local parrot abundance, but the relationship between flyway counts and actual densities has not yet been demonstrated. Flyway counts have been used as an abundance index to study seasonal population variation in the occurrence of macaws in Peru (Renton 2002). Amuno et al. (2007) used flyway counts to estimate local Grey Parrot abundance as a product of the mean number of flocks and flock sizes, and then inferred local abundance to a much wider area by estimating the possible number of flyways present. Nonetheless none of these methods has been tested empirically and their reliability as a surrogate for more accurate methods is open to question.

The number of birds flying along each of the surveyed flyways was different between sites, but relatively consistent in proportion to each other as well to the known total population estimate. Moreover, the daily variation was relatively small, ranging from 9% of São Joaquim to 17% in Bela Vista. These data suggest there may be scope for further investigation to find a more robust relationship with local densities. The flyways surveyed in Príncipe showed a clear unidirectional flow of birds that may avert the risk of overestimation owing to double-counting. The post-breeding season sees a larger number of individuals wandering away from the main flight direction, which may be due to different behaviour by the newly recruited juveniles, although it is hard to confirm this as ageing juveniles in the field is impossible (Dändliker 1992). Nonetheless the seasonal variations in the number of 'stray' individuals and in group sizes suggest that selecting the right period for the survey and making sure that timing of repeated counts is consistent may be crucial to the accuracy of the method for the long-term monitoring of parrot populations. The large differences between the

totals obtained from 1997–1998 counts and later ones highlight how failing to standardise the method may result in non-comparability of results and, in turn, in the missed opportunity of detecting reliably a possible population decline. More investigation is needed to evaluate the reliability of flyway counts as surrogates for density estimates. Nonetheless it is likely that the applicability of this method would be strongly limited to areas where a regular, consistent and unidirectional movement of parrots occurs.

3.5.4. Conclusions

Owing to the uneven distribution of resources and skills there is great scope for developing a wide range of methods for estimating animal abundance, to inform effective conservation actions in a array different situations. This is particularly true for Psittaciformes, which are disproportionately threatened and widely distributed in a variety of logistically difficult habitats. Nonetheless, distance sampling remains by far the most used and reliable method (Marsden and Royle 2015), and its application should be preferred wherever time, resources and skills allow it.

With so much variation in abundance across the ranges of parrots, different approaches are needed to maximise the knowledge of local and overall abundance. A hierarchical approach to surveying parrot species in general may be beneficial. In the case of grey parrots, for example, in areas such as the big parks in Cameroon and Gabon line transect distance sampling surveys will be feasible to estimate population sizes. In these cases, the use of carefully designed distance sampling surveys is, of course, preferable to less precise methods. The former considers local detectability issues and yields estimates of actual density and precision (Buckland et al. 2008). In more inaccessible areas such as Gabon and D. R. Congo, encounter rates may be more suitable as it may also be possible to 'piggyback' data collection with this method onto existing surveys, such as those for elephants and apes (e.g. Maisels et al. 2013). In such cases, it is crucial that adding parrots to the list of existing survey targets does not negatively impact field protocols or search techniques for those species. However, and in short, the ideal surveys for parrots are

those tailored specifically for them (Marsden 1999) and performed by properly trained fieldworkers (Nadeau and Conway 2012). It is also important to note, however, that areas which have high densities of large mammals may not necessarily coincide with those having high grey parrot densities, as was shown by the results from TL2 in D.R. Congo (Hart 2009). Finally where logistics and resources disallow the implementation of any of the above methods, if the area has the right geographical characteristics, long watch methods may be useful in getting a broad indication of parrot abundance, but mainly as a justification for further investigations carried out with more accurate and reliable methods.

3.6. Acknowledgements

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Chapter 4. Exceptionally high breeding density and output in an insular population of Grey Parrot *Psittacus erithacus*

4.1 Summary

Nest density and productivity, and the natural and anthropogenic influences on them, are important elements in our understanding of bird population dynamics, especially in heavily-traded species such as parrots. We identified, with the help of ex-trappers, 160 active Grey Parrot *Psittacus erithacus* nest cavities on the island of Príncipe. Unlike most areas in mainland Africa, Príncipe still holds a large and perhaps increasing population of parrots, despite a history of heavy trapping. We identified characteristics of 83 nests, estimated number of chicks fledged per nest cavity based on trappers' records, and calculated minimum nest site density across different forest habitats on the island. Nest sites were located in large living individuals of a small number of tree species (mostly *Cleistanthus sp.* in primary forest and *Erythrina variegata* in secondary forest). Nest productivity averaged 1.9 chicks per cavity and was not influenced significantly by forest type, tree characteristics or any of the other habitat elements measured. Minimum nest densities from two primary and five secondary forest sites were 72 and 16 nests km^{-2} respectively. These nest densities are far greater than those recorded for the species in mainland Africa, and indeed for any non-colonially nesting parrot species. The abundance of parrots on the island may be a function of high availability of potential nest sites, a lack of competition from hornbills and other cavity-nesters, and the inaccessibility of many nest sites to poachers.

4.2   Introduction

Breeding biology and performance represent an central aspect of the population ecology of birds and are critical in identifying effective conservation measures for threatened and declining species (Green 2004). This is particularly true for commercially exploited species, whose breeding output has to counterbalance the impact of a periodical harvest (Beissinger 2001). In many exploited species (e.g. gamebirds), annual yield is increased through breeding site supplementation or enhancement of breeding success to produce a harvesting excess (Getz and Haight 1989, Beissinger and Bucher 1992). Even in the absence of such measures, the investigation of productivity rates and of the factors that affect them is crucial to an understanding of resilience to harvest, and to inform population and habitat management (Beissinger and McCullough 2002).

Parrots (Psittaciformes) are among the most endangered bird orders, with 30% of species currently threatened (IUCN 2014), primarily owing to the effects of habitat loss/degradation and excessive trade (Snyder et al. 2000, BirdLife International 2014a). The majority of parrots nest in natural tree cavities, to which they may make only minor adaptations (Collar 1997). Their requirement for cavities in very large trees (Marsden and Jones 1997), or specific tree species (Marsden and Pilgrim 2003), is a cause for concern when these trees are the target of loggers (Nelson and Morris 1994), or are not being recruited due to a lack of regeneration (Manning et al. 2013). The importance of maintaining breeding output is crucial in enabling parrot populations to withstand harvest or other pressures, yet the specific nest requirements, success and nest densities are very poorly known for most species (Collar 1998). Nests are often high in trees, which makes it particularly challenging to find and monitor them (Casagrande and Beissinger 1997).

Grey Parrot *Psittacus erithacus* has a huge range in West and Central Africa, but has recently been uplisted to 'Vulnerable' (BirdLife International 2014b) on account of sharply declining populations across its range, and its virtual

extinction in some countries (Marsden et al. 2013). As with other parrot species, the causes of such dramatic declines are to be found in a combination of factors. Hundreds of thousands of individuals are harvested from the wild each year, to feed a multi-million dollar international pet trade (Beissinger 2001, UNEP-WCMC 2014). Concurrent with this direct exploitation is the loss and degradation of tropical forests (Hansen et al. 2008). Remarkably, the island of Príncipe in the Gulf of Guinea is home to a population of Grey Parrots that is still large (densities around 50 birds km^{-2}; Marsden et al. 2013), and perhaps increasing, despite a long history of heavy trapping (Juste 1996). Given a population trajectory so different from that of Grey Parrot populations elsewhere, it is important to examine the nesting ecology of the species on the island.

The objectives of this study were to (1) examine nest site selection on Príncipe and compare it to that elsewhere in mainland Africa, (2) identify nest productivity on the island and factors influencing it, and (3) determine likely nest densities in intact and disturbed forests and to compare these to densities in mainland parrots.

4.3   Methods

4.3.1 Study area

The island of Príncipe (1°32'–1°43'N 7°20'–7°28'E) lies 220 km off the coast of West Africa, in the Gulf of Guinea, and covers an area of 139 km^2 (Fig. 1). The region has an oceanic equatorial climate regulated by the interaction of the southern monsoon winds from the Atlantic Ocean with the Intertropical Convergence Zone (Melo 2004). The natural habitat of Príncipe island has been described as lowland rainforest (Exell 1973), or tropical moist broadleaf forest (Olson and Dinerstein 2002). The island had been uninhabited until its discovery in 1471, after which all accessible areas have been cleared and planted with cocoa, coffee and coconut, but most of the southern half of the island has been left untouched (Jones and Tye 2006). Príncipe has a

typically depauperate fauna, with 36 breeding birds, few native mammals (i.e. four species of bats and one shrew) and no real predators, but high levels of endemism (Jones 1994). A number of mammal species had been introduced (e.g. Mona Monkey *Cercopithecus mona*, Brown Rat *Rattus norvegicus*, etc.), and their impact on native fauna is not yet known (Dutton 1994).
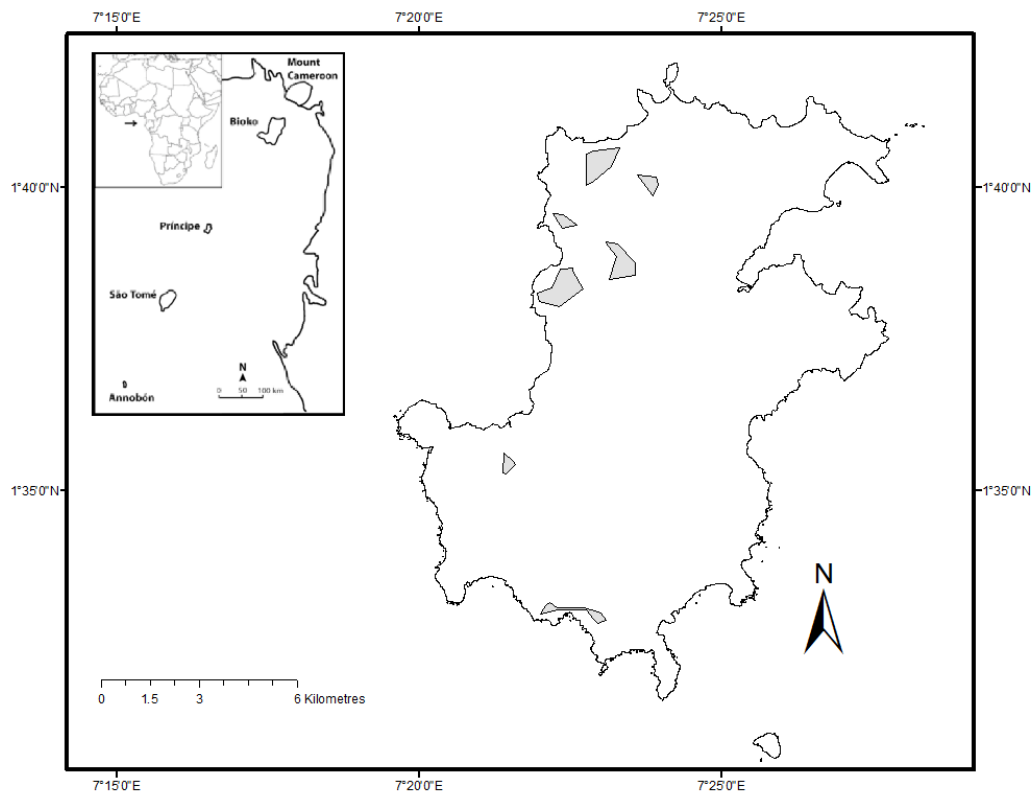
Fig. 4.1 Map of the Island of Príncipe and its position within the Gulf of Guinea. Shaded in grey are the seven clusters of nests studied

The Grey Parrot is a very popular pet species. From 1982 to 2001, over 650,000 wild-caught individuals entered international trade (UNEP-WCMC 2014), with Cameroon being the main exporter with 367,166 individuals legally exported between 1981 and 2005 (BirdLife International 2014b). Real figures could be much higher since illegal trade is not accounted for. Together with the loss/degradation of its habitat, the volume of capture has caused a major collapse of populations in the wild (BirdLife International

2014b). Despite being a valuable species on the market, however, virtually nothing is known of its ecology in the wild and particularly of its breeding biology (Juniper and Parr 2003). Nest densities are known only from one study i.e. 1.3 nests km-2 (SD = 0.13) in Nigeria (McGowan 2001). Although it has been known to nest in rock cavities (Marsden et al. 2013) or even buildings (Twanza and Pomeroy 2011), the Grey Parrot can be considered an obligate tree-cavity nester, making it particularly vulnerable to a low availability of suitable cavities due to tree-felling or competition.

4.3.2 Nest surveys

In Príncipe, parrots have traditionally been harvested as chicks, and local trappers have knowledge of the location of tens of nests found over decades of catching activity in the forest (Melo 1998). Thus, all nests examined in the present study, apart from two newly-found ones, were known and regularly harvested by local trappers. Eighty-three nests were inspected in two distinct types of forest, i.e. 39 in primary forest and 44 in secondary forest, between November 2012 and April 2014. The exact locations of 80 nests had been collected, using the same method, by MM in 1998 in two further areas of primary forest. It was not possible to verify systematically if the nests were in use or not, although most of them had be known to be active at the same time in previous seasons.

For the 83 nests examined in 2014, the following measures were taken: GPS coordinates, altitude, nest height (measured with a clinometer and a rangefinder), whether the nest opened to one side of the tree or upwards, orientation of the nest aperture (8-point compass rose), tree species (Figueiredo et al. 2011), tree height (clinometer and a rangefinder), diameter at breast height (estimated), and health status of the tree (following Saunders et al. 1982). Some tree species could be identified by the local name only. Tree species and DBH of the largest three trees were recorded in 103

vegetation sample plots of radius 20 m, randomly located across the island. Estimates of tree DBH were periodically checked with a tape measure.

For each of the above nests, data were collected on the number of chicks harvested in the last known breeding season (hereafter referred to as 'nest productivity') by interviewing the trapper who historically harvested from the nest. Interviews were conducted at the nest tree itself. Although it is impossible to assess the accuracy of the parrot trappers' information, there is no obvious or plausible reason for them to misrepresent the truth. Moreover, the reported number of chicks per nest is consistent with existing data on the reproduction of the species on the island (Juste 1996). Data on productivity were not available for three nests as they had been found in the same year of the survey. The distance from each nest to the nearest other nest was measured with ArcGIS 10.1 (ESRI 2012).

4.3.3 Analysis

Analysis of the direction that each cavity aperture faced was performed with the circular statistics package 'circular' in R (R Core Team 2014), and their homogeneity was tested with the Rao's Spacing Test. The probability of nesting in a certain tree species according to its local availability was calculated as the frequency of occurrence of that species among the closest nine trees with a DBH ≥ 20 cm. A Mann–Whitney U test was used to test difference in tree girth between nest trees and the biggest trees of the same species across the island. The analysis was carried out independently for the two most common nest species (accounting for 51% of all nests) while the rest of the species were pooled in one analysis. A further analysis was performed for all tree species together. A Kruskal–Wallis one-way analysis of variance was used to test whether nest height or nest-tree DBH influenced nest productivity, and a chi-squared test was used to test if the number of chicks fledged was randomly distributed between primary and secondary forest or between tree species.

To estimate the minimum nest density, nests were grouped into seven clusters (five in secondary and two in primary forest, Fig.1) of three or more points within an aggregation distance of 1 km, using ArcGIS. A minimum convex polygon (MCP) was drawn around each cluster, surrounded by a buffer zone area of width half of the mean minimum distance between nests for that cluster (Wilson and Anderson 1985). Within each cluster area, thirty 50 m radius circular sample areas were randomly created, and within each of these, nest density was calculated. Minimum nest density was averaged for each cluster. Mean density values for each cluster were averaged for each forest type. Finally, to compare our nest densities with those on Grey Parrots and other parrot species, available literature was reviewed using Web of Knowledge, Google Scholar, and a manual search of more than 2,400 references stored in the Parrot Research Group library.

4.4   Results

4.4.1 Nesting requirements

Nest cavities were found in 13 tree species, principally *Erythrina variegata* (34%), *Cleistanthus* sp. (17%), Pau Carteira (16%), *Pentaclethra macrophylla* (12%), Gogo Bravo (7%), *Zanthoxylum gilletii* (5%) and other species (10%), i.e. tree species which vary greatly in availability and ubiquity across the island (Table 1). Parrots selected their nesting tree species according to their local availability ($\chi^2 = 11.4$, df = 10, $P = 0.33$). Mean nest height was 24.5 ± 8.3 m (mean ± SD), with the lowest and the highest being 7 m and 57 m high respectively. Nest-tree height was between 20.9 m and 91.1 m (mean ± SD = 45.3 ± 14.0 m), with a DBH ranging from 0.50 to 2.80 m (mean ± SD = 1.22 ± 0.49 m). Tree height was significantly correlated to DBH (r = 0.23, df = 81, P < 0.05), so only the latter was used in subsequent analysis. Nests were higher and in larger trees, in primary forest than in secondary forest (t_{80} = 4.12, P < 0.001 and t_{81} = 3.73, P < 0.001 respectively). All but four nests were in living trees (two partially dead or dying trees, and two trees which

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were said to have died long after the birds had started nesting in them). Nests could be as close as 15 m from one another. Nests openings were usually to one side of the tree (71%) rather than opening upwards (29%). The orientation of laterally-facing nest cavities was not significantly different from random ((Rao's $U = 0.51$, df $= 1$, $P = 0.47$, Fig.2). Nests mainly faced South (11, 19.0%), North and East (10 each, 17.2%), Northeast (9, 15.5%) and Southeast and Southwest (6 each, 10.3%), while few were orientated towards West or Northwest (6, 10.3%). Apart from *Erythrina variegata*, the girth of nest trees was significantly larger than the girth of largest trees of the same species measured across the random plots (Fig. 3).
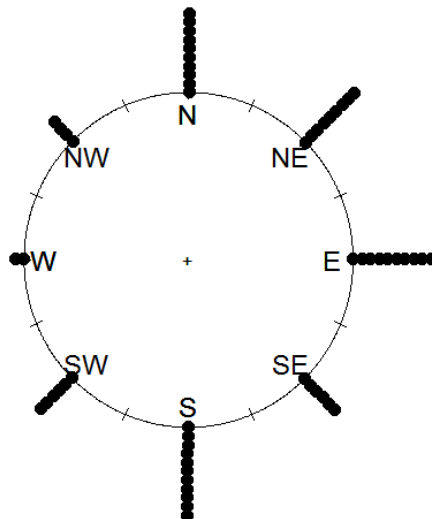
Figure 4.2. Circular distribution of the aperture orientation of Grey Parrot nests in Príncipe (nests opening upwards excluded)
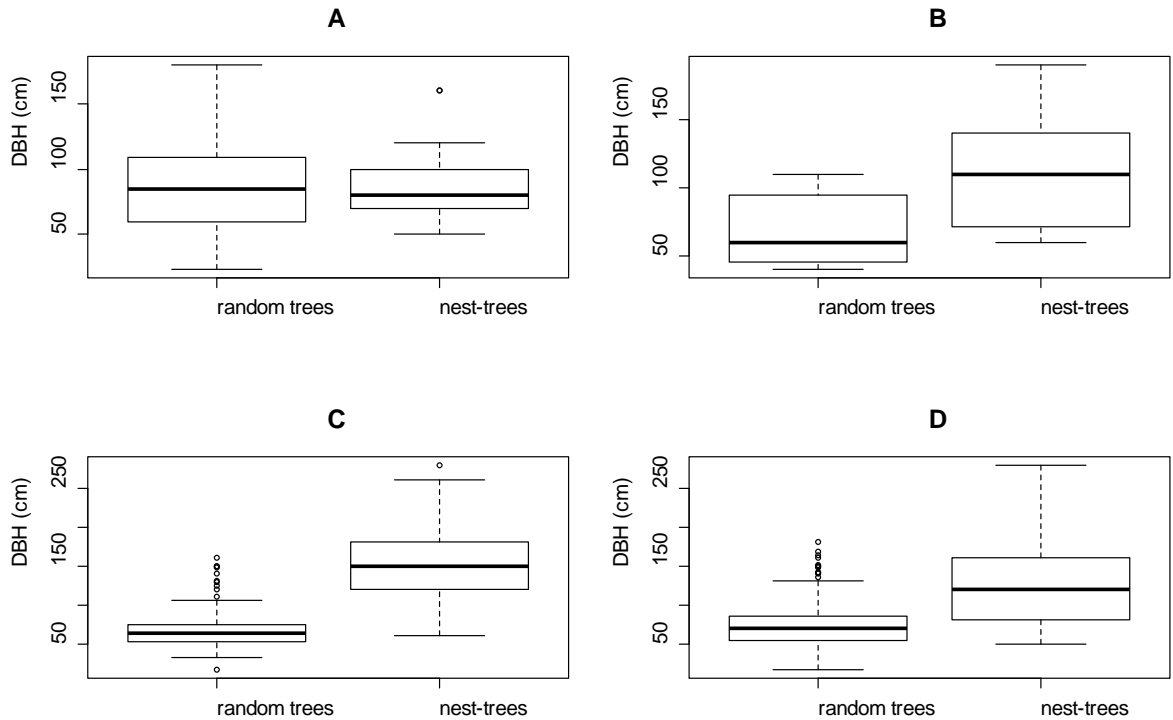
Figure 4.3. Differences between girth of Grey Parrot nest trees and random individual trees for A. Erythrina variegata (W = 815, P = 0.98), B. Cleistanthus sp. (W = 22, P < 0.05) and C. all remaining species (W = 270, P < 0.001, and D. for all species pooled together (W = 2873, P < 0.001)

4.4.2 Nest productivity and density

Nests were said to have produced between one and three chicks (mean ± SD = 1.94 ± 0.7, n = 81). Nest productivity did not differ between primary and secondary forest (t_{78} = 0.1, P = 0.92) or between differently orientated nests (circular-linear regression, t_{57} = 0.13, P = 0.4), nor was it influenced by DBH (χ^2 = 15.2, df = 19, P = 0.71), nest height (χ^2 = 76.86, df = 72, P = 0.32) or tree species (χ^2 = 4.54, df = 4, P = 0.34). Mean minimum nest densities for secondary forest and primary forest were 16.8 ± 7.9 (mean ± SD, range 8.8 – 26.3) and 72.4 ± 26.2, (mean ± SD, range 39.5–101.0) nests km^{-2} respectively.

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Table 4.41. Tree species used for nesting by Grey Parrot according to literature or local knowledge, number of nests found in each species, 'availability' of each species as mean number of suitable individuals (DBH≥ lower quartile of DBH of nest trees for the same tree species) per vegetation plot (n = 103) and percentage of total number of trees measured in the vegetation plots across the whole island (n = 302); ubiquity as percentage of vegetation plots in which the species appears; preference for each species as % of nests of total on % of availability; and literature referring previously to use of the species for nesting.

Species	Nests (%)	Availability (%)	Ubiquity	Preference	Reference
Erythrina variegata	28 (34)	0.36 (12)	30	2.8	Juste 1996
Cleistanthus sp.	14 (17)	0.03 (1)	5	17	Juste 1996
Pau Carteira	13 (6)	0.01 (0.3)	6	47	
Pentaclethra macrophylla	10 (12)	0.04 (1)	16	9.1	
Gogo Bravo	6 (7)	0	4	0	
Zanthoxylum gilletii	4 (45)	0.01 (1)	9	15	Juste 1996
Santiria trimera	2 (2)	0.01 (1)	6	7.3	
Dracaena arborea	1 (1)	0	2	0	
Pauridiantha floribunda	1 (1)	0	18	0	
Pau Candeia	1 (1)	0	4	0	
Polyalthia oliveri	1 (1)	0	2	0	
Pseudospondias microcarpa	1 (1)	0	4	0	
Xili xili	1 (1)	0	14	0	
Milicia excelsa	0	0.02 (0.7)	3	n.a.	Juste 1996 Dandliker 1992

4.5 Discussion

Grey parrots on Príncipe nested in large live individuals of particular tree species, a selection quite typical of the species elsewhere in its range (Dändliker 1992; Amuno et al. 2010), and indeed of larger parrot species across the tropics (Marsden and Jones 1997; Mawson and Long 1994; Monterrubio-Rico et al. 2006). While there was nothing extraordinary about nest site selection on the island, the likely densities of nest sites is. The only other estimate of nest density in grey parrots is 1.3 ± 0.13 nests km^{-2} (mean $\pm$ SD, range 0.5–2.1) from Nigeria (McGowan 2001). Thus, our figures, at more than 70 nests km^{-2} in some areas of the island, are the highest ever recorded for any native, non-colonial, tree-nesting parrot species (Table 2). Of course, nesting density is little studied in parrots but the scale of the difference between densities on Príncipe and those elsewhere is striking. Such high breeding densities could be the product of one or more factors:

In Príncipe there is limited number of bird species competing in a resources-rich and environment (Jones and Tye 2006). This may result in a 'density compensation' effect, where, the summed high population densities of the few species on islands, is similar to the summed lower densities found on species-rich mainland (MacArthur et al. 1972). This has been found to be the case for the avifauna of several tropical islands (Wright 1980).

Nest trees selected by Grey Parrots on Príncipe were all common and widespread on the island. Large portions of Príncipe have been left virtually untouched, owing to their inaccessibility, and at least 45% of its surface is covered by mature lowland forest (Jones and Tye 2006). The remainder of the island has mainly been used for shade plantations of coffee and cocoa (Albuquerque et al. 2004), which provide food (e.g. oil palm *Elaeis guineensis*) and retain old forest trees and generally high levels of biodiversity (Perfecto et al. 1996, Faria and Baumgarten 2007).

In Príncipe, Grey Parrot is the only large hole-nesting vertebrate (Jones and Tye 2006), freeing it from interspecific competition for cavities, a known

limiting factor for many bird species (Martin and Eadie 1999, Strubbe and Matthysen 2009). Particularly important may be the lack of hornbills (Bucerotidae), the most likely competitors for nest sites over much of the Grey Parrot's range. Indeed, the only documented instance of natural predation on a Grey Parrot is of a Black and White Casqued Hornbill *Bycanistes subcylindricus* killing a brood in order to take over the cavity for breeding (Kalina 1988). Moreover, a suite of tree-dwelling mammals (e.g. Galagidae, Viverridae, Muridae, Mustelidae) must also provide significant competition in mainland West and Central Africa, but again, are absent from Príncipe.

Besides the introduced Mona Monkey, which may prey opportunistically on unguarded nests (Jones and Tye 2006), there are no nest predators on Príncipe (Dutton 1994). Nest predation can seriously affect productivity and density in parrots (Britt et al. 2014), and in mainland Africa, the same mustelids and viverrids that compete for cavities are also predators on hole-nesting animals, as are various arboreal primates and snakes (e.g. Patas monkey *Erythrocebus patas,* Chimpanzee *Pan troglodytes*, African Rock Python *Python sebae*).

For many parrot species, poaching is the primary source of nest failure (e.g. Wright et al. 2001). Despite a history of heavy trade, with up to 1,500 chicks exported annually in the 1990s (Juste 1996), Príncipe still hosts high densities of Grey Parrots, and it always seems to have done (Jones and Tye 2006, Melo and O'Ryan 2007, Marsden et al. 2013). Traditional trapping methods on Príncipe usually involve harvesting chicks from the small proportion of cavities which are known, the locations of which are passed on from generation to generation (Melo 1998). Our data indicate that productivity per nest is likely to be high, but more importantly, a high density of nests, and the inaccessibility of many of them on the island, has enabled its parrots to withstand a harvest that effectively took up to eleven parrot individuals annually from each of its 139 km^2 of land area. Whether nesting densities on Príncipe are truly exceptional, or whether mainland populations could

achieve such productivity, is not known. Most Grey Parrot populations across its huge range are thought to have collapsed (Martin et al. 2014). An exception is Lobeke NP, and perhaps other well-managed protected areas in Cameroon where parrot densities may reach 10-30 individuals km^{-2}, not dissimilar to those on Príncipe (around 50 birds km^{-2}; Marsden et al.2013). A priority for research would be to examine likely nesting density in these areas to determine if their parrot populations are productive, and if not, what can be done to aid them. Ultimately the success of Príncipe's Grey parrot population in withstanding harvest pressure, as in other parrot populations (Beissinger 2001), is a high breeding output facilitated by high densities of successful nests.

4.6   Acknowledgements

Table 4.62. Nest densities (nests km-2) for parrot species in previously published studies and the current study.

Species	Location	Density ± SD (range)	Habitat type	Reference	Methods/notes
Hyacinth Macaw *Anodorhynchus hyacinthinus*	Pantanal, Brazil	0.045	Savanna, forest patches flood plains	Pinho & Nogueira 2003	Methods not described
Blue-fronted Amazon *Amazona aestiva*	Pantanal, Brazil	0.26 ± 0.3 (0.03 – 0.5)	Savanna, forest patches flood plains	Fernandes Seixas & Mourão 2002	Active nests located by following individuals from high parrot concentration areas and, in some cases with information from trappers
Grey Parrot *Psittacus erithacus*	Nigeria	1.3 ± 0.13 (0.5 – 2.1)	Various	McGowan 2001	Nest density calculated from local trappers' knowledge. Minimum nest density.
Scarlet Macaw *Ara macao* Blue and Gold Macaw *Ara ararauna* Green-winged Macaw *Ara chloroptera*	Manu NP, Peru	6.1	Rainforest	Nycander et al. 1995	Nest/cavity search. Density calculated across all species through extrapolation.
Grey Parrot *Psittacus erithacus*	Príncipe	41.5 ± 33.9 (8.8 – 101.0)	Lowland rainforest	This study	Nest density calculated from local trappers' knowledge. Minimum nest density.

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Chapter 5. Using scenarios to predict effects of harvest and habitat loss on a population of Grey Parrots *Psittacus erithacus*

5.1 Summary

Population Viability Analysis (PVA) is a useful tool for modelling population dynamics and predict likely population trends in the face of decline. A PVA model was built to study a population of Grey Parrots *Psittacus erithacus* on the island of Príncipe, and infer the species' sensitivity to two main, and often concurrent, threats, namely the harvest for the pet trade and habitat loss. The model was first used retrospectively to understand the likely trajectory of the population in the last 20 years. In Príncipe, Grey Parrots have been slowly declining through years of intense harvest, but are now steadily recovering after a ban on the trade was put in place in 2005. The species displayed good recovery potential, although a number of environmental factors may have particularly favoured this in Príncipe. Adult survivorship was found to be a most critical demographic parameter to the population persistence, more than juvenile survivorship and nest success. This was not unexpected considering the biological characteristics common to most long-lived slow-breeding species. The model was then used to investigate a number of hypothetical future harvest and habitat change scenarios. Effects of harvest were shown to be unimportant only if strict conditions applied, i.e. a small and consistent number of chicks only was yielded yearly from a large and healthy population. The possible sustainability of chick harvest was discussed in the light of the limitations of the model, and social and political factors which are hard to quantify. Destruction of habitat was proved to affect the maximum possible size of the population, but not its extinction risk. The species was shown to have the potential to survive in low densities in small and isolated areas of suitable habitat (e.g. protected areas), although it was highlighted how these may often be, in reality, cases of delayed extinction. Finally the interaction between

the concurrent effects of harvest and habitat loss was explored. It was highlighted how these affect the population through different demographic mechanisms, which would be difficult to detect in field studies. Despite the limitations PVA models proved to be a useful tool for the study of parrot populations, as they offer the opportunity to quantify the effects of coexisting threats, and help to prioritise conservation efforts.

5.2   Introduction

Population Viability Analyses (hereafter PVA) are stochastic simulation models that use demographic data from a population to make quantitative predictions about its size and likelihood of extinction over time (Beissinger and McCullough 2002). PVAs were first developed in the 1980s to assess the extinction risk of species which had been reduced to very small populations (Gilpin 1996), and have since been widely used to inform conservation management of different taxa (Norton 1995). PVAs have proved particularly helpful in understanding the effects of anthropogenic harvest, and in exploring the possibility of managing wild animal populations to implement sustainable quotas (Beissinger and Bucher 1992b). PVAs have the potential to help conservation scientists to separate the effects of anthropogenic factors from those of natural ones, providing constructive insight into which ones most affect population growth or decline (Reed et al. 2002). Nonetheless, the building of a good PVA model requires significant knowledge of the life history traits (e.g. survival, fecundity, maximum lifespan) of the study species, which is often unavailable and difficult to obtain (Beissinger and Westphal 1998). Despite the difficulties in estimating life-history parameters and validating the models empirically, PVAs can be extremely useful to conservation biologists as a secondary source of analysis, if results are cautionarily interpreted in terms of uncertainty (Reed et al. 2002). PVAs' greatest and most useful contribution might be to allow the simulation of an array of possible scenarios through the methodical variation of key parameters in the model, and evaluation of their effects on a given population (i.e. sensitivity analysis; Mills and Lindberg 2002). For example, changes in land use may affect populations of different species according to different factors such as limiting available nest sites (Newton

1994), or territories (Lamberson et al. 1994), decreasing the adult survival and fecundity (Akçakaya and Atwood 1997), or changing sex-ratio (Kruuk et al. 1999).

The Psittaciformes are among the most endangered orders of birds (IUCN 2014), and the decline of most of the worlds' parrot populations is believed to be driven by a combination of two main factors: the rapid loss and alteration of their habitat, and the harvest for the international pet trade (Snyder et al. 2000). Juniper and Parr (2003) estimated that habitat loss alone affects 73 of the species currently endangered, that trapping for the pet trade alone affects 39 species, and that 28 species experience both forms of pressure. While listing potential threats is straightforward, determining the precise contribution of each of the concurrent factors to species declines, and how their effects intertwine, is far more difficult (Collar and Juniper 1992).

Despite their conservation status, and their popularity among the general public, parrots are a seriously understudied group owing to their distinctive biological characteristics, namely slow breeding performance, wide-ranging behaviour, unpredictable foraging movements, non-territorial habits and virtual invisibility when perched (Collar 1998). As a consequence, little is known of parrot population dynamics and how they may change over time in response to different threats. PVAs have been used to study population dynamics of parrot species in the face of a wide range of threats, from habitat loss (Koenig 2008, Heinsohn et al. 2009) and introduced predators (Heinsohn et al. 2015) to climate change (Harris et al. 2012) and trade (Bouzat and Strem 2012). PVAs have been particularly useful in understanding how harvest for the pet trade affects parrot populations (Beissinger and Bucher 1992a). Demographic models like PVAs have the potential to be the founding basis for those 'non-detriment findings' which ought to insure that the exploitation of any given species is sustainable as ratified by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 2015). The Grey Parrot *Psittacus erithacus* has suffered a dramatic population decline in the last twenty years owing to its popularity on the pet market and the rapid destruction of its habitat (BirdLife International 2014). Nonetheless, little is known about the species' ecology and the demographic processes by which different types of anthropogenic pressure affect wild populations (BirdLife International 2014). Thus, a

better understanding of Grey Parrot population dynamics has become a crucial priority to inform management of the species and keep harvest at a sustainable level if possible (CITES 2013).

A stage-based model was developed for an abundant and isolated population of Grey Parrots in Príncipe, a West African island with a long history of harvest for the pet trade (Juste 1996, Melo 1998). The model was first validated empirically and then used to simulate hypothetical scenarios and study how the population would be affected in the medium and long term by: 1. variation in some key demographic parameters such as survivorship and nest success; 2. different degrees of harvest pressure; 3. different extent of habitat degradation and loss; and 4. a range of harvest quotas met through a suite of possible techniques combined with the effects of habitat disruption.

5.3 Methods

5.3.1 Model development

The total absence of annual survival data precluded development of an age-based model, so a stage-classified population model was developed instead (Caswell 1989). This type of model use a Lefkovitch matrix which takes into account the two different possible transitions from one class to another, i.e. surviving and remaining in the same age class, or growing into the next one. A female-based model of the population of Grey Parrots in Príncipe, as females are the limiting sex for breeding and the inclusion of both sexes are likely to underestimate the true extinction risk (Brook et al. 2000). The model was developed on the basis of three stage classes: juveniles (from birth to one year of age), sub-adults (from one till the reaching of sexual maturity at three years of age) and adults (from four years of age). The model is based on a 3×3 Lefkovitch matrix, structured as follows:

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$$
\begin{matrix}
P_1 & F_2 & F_3 \\
G_1 & P_2 & 0 \\
0 & G_2 & P_3
\end{matrix}
$$

In this matrix, for each given stage i, P_i is the probability of surviving and remaining in the same stage, G_i is the probability of surviving and growing into the next stage, and F_i is the stage-specific reproductive output.

The distribution of individuals within a stage, and their subsequent probability of progressing to the next age-class, is determined by the stage length in years and the annual survivorship probability for that stage. The model assumes a stable age distribution within each stage. The annual probability of an individual growing into the next stage (γ) is calculated by:

$$
\gamma = \frac{\left(\frac{\sigma_i}{\lambda}\right)^{T_i} - \left(\frac{\sigma_i}{\lambda}\right)^{T_{i-1}}}{\left(\frac{\sigma_i}{\lambda}\right)^{T_i} - 1}
$$

where i is the stage number, σ is survivorship and T is the duration of the stage in years. λ is an initial estimate of the increase or decline rate calculated as:

$$
\lambda = \sqrt[i]{\frac{N_{t+i}}{N_t}}
$$

Thus, the matrix transition parameters were estimated as follows:

$P_i = \sigma_i \times (1 - \gamma_i)$

$G_i = \sigma_i \times \gamma_i$

$F_i = (\text{fecundity}_i \times P) + (\text{fecundity}_{i+1} \times G_i)$

A one-year simulation is performed by multiplying the matrix by a population vector:

$$N = \begin{matrix} N_1 \\ N_2 \\ N_3 \end{matrix}$$

where N_1, N_2 and N_3 are the initial number of individuals estimated for the first, second and third age-class respectively. A proportion of the individuals in N will make a transition into the following age-class according to the probabilities enbedded in the matrix. The resulting vector is then multiplied again for the matrix and the operation is repeated a number of times equal to the number of subsequent years for which the simulation is set. Each simulation process was run 1,000 times. The development and the implementation of the model were performed with R software (R Core Team 2014; see Appendix I for script) .

5.3.2 Model implementation and validation

For a number of reasons (e.g. difficulty of marking birds individually, short duration of research projects compared to the species biological cycle, trouble in estimating population densities), quantifying parrots' specific life history traits is often problematic (Beissinger 2001). Grey Parrots are no exception and very little is known on these traits in the wild, so the model has been run using a combination of data collected from Principe itself (see Chapters 2 and 4), information about the same species elsewhere within its range (e.g. Nigeria, Cameroon), field data from other

analogous parrot species, and data on *P. erithacus* from captivity (Young et al. 2012).

On Príncipe, owing to its isolation from São Tomé and the mainland, the Grey Parrot population can be assumed to have no immigration or emigration (Jones and Tye 2006), thus it can be considered a **closed biological population** i.e. a group of interbreeding organisms found in the same space or area (i.e. they are sympatric) at the same time (Rockwood 2006).

The **finite rate of population increase** (the growth rate per time period, usually per year; Rockwood 2006) λ, was calculated from the increase in the results of the pre-breeding population counts from 2014, compared to the ones from 2012, as follows:

$$\lambda = \sqrt[9]{\frac{936}{273}} = 1.1$$

Grey Parrots, like most Psittacidae, are known to be **long-term monogamous** (Forshaw 1989, Seibert 2006). All adults capable of breeding are assumed to do so as long there are sufficient nest sites available (see below '*number of available nest sites*').

In captivity**, the age of first breeding** can vary greatly, depending on husbandry conditions, i.e. median (± interquartile range) = 7.6 (5.4–9.5) (Young et al. 2012). Nonetheless, it is known that Grey Parrots usually reach sexual maturity between their third and fifth year of age (De Grahl 1987, Silva 1991, Lantermann 2000). In the model, the fourth year was considered the threshold of adulthood; thus the subadult stage comprises two- and three-year-old individuals.

Grey Parrots are known to breed once per year throughout their range (Benson et al. 1988), so each simulation allowed for one yearly **brood**. Productivity for successful nests (**fecundity**) was inferred from the study of 81 nests on Príncipe (see Chapter

4; mean ± SD of 1.96 ± 0.72 **chicks per brood)**. As information from the island suggested that inter-annual variability in productivity was low (Chapter 4), this was set nominally to 0.1. A review of sex ratios at birth showed that Grey Parrots have a **ratio of females to males** of 46% (n = 3,892, χ^2 = 25.01, p < 0.001; Taylor and Parkin 2008). A summary of the life history traits used in the model is given in Table 3.

No data are available on Grey Parrot survivorship in the wild, so this was inferred from the available literature on the survivorship of other parrot species in the wild (Table 1). It is known that longevity is positively correlated body mass (Brouwer et al. 2000, Young et al. 2012) and to adult survivorship (Lindstedt and Calder 1976). Thus, the mean (± SD) **survivorship** from three species, whose mean body mass is closest (i.e. ≤ 60 g. difference) to that of Grey Parrots (Western Corella *Cacatua pastinator*, Major Mitchell's Cockatoo *Cacatua leadbeateri*, Glossy Black-cockatoo *Calyptorhynchus lathami*) was used for the model i.e. 50 ± 0.8% for the first year of life and 91 ± 0.3% for birds older than one year, assuming that subadults, as fully formed and, thus, physically able individuals, share the same survivorship with adults.

Table 5.31. Information of parrot survivorship (%) in the wild currently and mean body mass (Del Hoyo et al. 2015) currently available in scientific literature (* the species used to infer on Grey Parrot survivorship).

Species	1st year	> 1st year	Weight (g)	Reference
Monk Parakeet *Myiopsitta monachus*	61	81	115	Pruett-Jones et al. 2007
Green-rumped Parrotlet *Forpus passerinus*	-	56.5	24	Sandercock et al. 2000
Orange-bellied Parrot *Neophema chrysogaster*	56	65	42	Holdsworth et al. 2011
Western Corella *Cacatua pastinator* *	51	93.5	500	Smith & Rowley 1995
Mitchell Cockatoo *Cacatua leadbeateri* *	44	87	420	Smith & Rowley 1995
Lilac-crowned Parrot *Amazona finschi*	73	73	297	Salinas-Melgoza & Renton 2007
Swift Parrot *Lathamus discolor*	55	71	62	Heinsohn et al. 2015
Puerto Rican Parrot *Amazona vittata*	68	-	275	Snyder et al. 1987
Glossy Black-cockatoo *Calyptorhynchus lathami**	61	91	450	Harris et al. 2012
Palm Cockatoo *Probosciger aterrimus*	29.4	66.3	775	Heinsohn et al. 2009
Black-billed Parrot *Amazona agilis*	70	90	178	Koenig 2008

A **nest success** rate of 77% was calculated from all the relevant available literature on parrots (see Appendix II) as the mean percentage nest success rate weighted by the number of nest years. It is assumed that the availability of nest sites is the one which may limit the yearly number of chicks. A limiting factor of the population was considered to be the **number of available nest sites** as this would directly affect the mean fecundity of the population, as shown in other parrot species (Beissinger and

Bucher 1992b, Munn 1992). A maximum number of available nest sites (5,502 ± 2,132 nests) was inferred from the mean minimum density of nests for primary and secondary forest, i.e. 72 ± 26 (SD), and 17 ± 8 nests km^{-2} respectively (see Chapter 4). Nest availability was modelled as a theta-logistic curve described by the equation

$$ y = F \times \left(1 - \frac{x}{nests}\right)^{\theta} $$

where F is fecundity, x is the number of adult females present in the population, $'nests'$ is the maximum number of available nest sites (i.e. minimum nest density + SD) and equals 10 (Fig.1).

Available nest sites
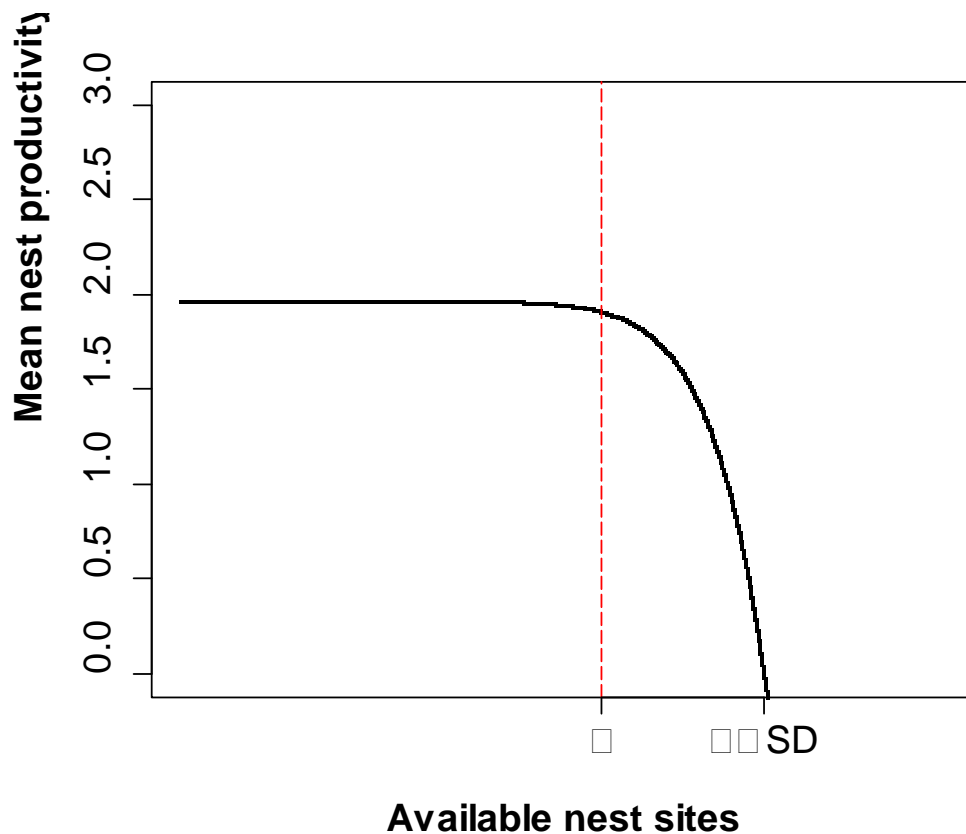
Figure 5.1. Decrease of mean nest productivity in relation to the mean nest density for the island (μ), and the assumed maximum number of nest sites available (i.e. μ+SD) according to a theta-logistic curve with θ = 10.

As the number of suitable nests (μ) are occupied and less suitable ones are used until the maximum available (μ+SD), the mean nest productivity is assumed to

decline. Thus, for each successive year and for each simulation, fecundity values were adjusted to the number of available nests through the integration of the above function, i.e.

$$\int_0^{\le nests} F \times \left(1 - \frac{x}{nests}\right)^{\theta}$$

Nest availability was the only density-dependent mechanism set in the model. The next most likely factor limiting population growth is the access to sufficient food resources, a parameter difficult to quantify and predict, because is heavily dependent both on fine habitat characteristics (i.e. floristic composition and plantation quality), and the ability of Grey Parrots to adapt to them. Since the focus of the analysis was to inform management of small and declining populations, we did not set any further arbitrary **carrying capacity** to the model.

The order Psittaciformes includes species with exceptionally long lifespans for their size (Holmes et al. 2001). In captivity, Grey Parrots' lifespan varies greatly according to the conditions in which they are kept (median = 8.2; IQR = 5.8–12.2; maximum = 48; n = 1,979; Young et al. 2012). There are no data on Grey Parrot lifespan in the wild, thus a generous **maximum lifespan** of 45 years of age was used in the model, as it is likely that adults would die before owing to a mortality rate higher than in captivity (Brouwer et al. 2000). Grey Parrots, at least in captivity, are known to be active breeders until they are very old (i.e. median = 8.8; IQR = 4.4–11.8, minimum = 1.75 [n = 14]; Young et al. 2012). Although it is likely that reproductive output may decrease in senescence, no data is available on this, thus the model assumed that parrots' lifespan and age of last breeding coincided.

Initially, the model was validated running a simulation for the 1995–2014 period, for which the Grey Parrot population trajectory is 'known' from the flyway counts (see Chapter 3). Initial population size (1995) was set to 3,911 (i.e. 1,799 females), assuming a constant mean ratio between flyway counts and actual population sizes (see § 3.4.4). Juveniles, subadults and adults were set at a ratio of 1:2:2.5, as this ratio resulted from a first run of the model with an initial adult-only population.

Population sizes for the years 2012 and 2014 were estimated with distance sampling (see § 2.3.2). Harvest pressure was set to 600 ± 50 chicks for the first 10 years (until the ban was enforced in 2005) according to the best available information (Juste 1996, Melo 1998).

Table 5.32. Parameters of the model used to validate the population model for Grey Parrots on Príncipe.

Life history trait	Value used in the model
Number of iterations	1,000
Number of year modelled	20 (1995–2014)
Number of population modelled	1
Inbreeding depression	No inbreeding depression assumed
Immigration rate	N/A
Emigration rate	N/A
Reproductive system	Long-term monogamy
Age of first reproduction	4 years
Maximum age of reproduction	45 years
Maximum lifespan	45 years
Maximum number of broods / year	1
Maximum number of progeny /brood	3
Mean number of chicks per brood ± SD	1.96 ± 0.76
Nest success	77%
Female : male ratio at birth	46%
Density dependence in reproduction	Availability of nest sites = 5,502 ± 2,132
Proportion of adult females breeding	All
λ - finite rate of increase	1.1
Juvenile survivorship	52 ± 0.8%
Subadult survivorship	91 ± 0.3%
Adult survivorship	91 ± 0.3%
Initial population size	Various depending from simulation
Age distribution (%) of initial population	1:2:2.5
Carrying capacity	None
Number of juveniles harvested	600 ± 100
Number of subadults harvested	0
Number of adults harvested	0

5.3.3 Modelling Grey Parrot demographics and future scenarios

Grey parrot population dynamics

All simulations were performed using an initial population size of 7,996 individuals (3,678 females) as estimated from the 2014 post-breeding surveys (see Chapter 2), unless otherwise stated. The model was used to predict the trend for Príncipe's Grey Parrot population in the next 50 years under actual conditions, i.e. no harvest and unchanged habitat. A sensitivity analysis was performed to understand how responsive the population trajectory was to changes in key demographic parameters. These were sequential 10% decreases in juvenile survivorship, 3% decreases in subadult and adult survivorship, and 15% decreases in nest success.

Response to harvest pressure

In agreement with the island tradition on harvesting almost exclusively chicks from nests, the model was run with a simulated annual harvest of 300 ± 50, 600 ± 100 (which to the best of our knowledge is the number of individuals harvested before the ban was put in place), 900 ± 100 and 1,200 ± 100 chicks. Standard deviations were set arbitrarily, but based on anecdotal evidence (S.Valle unpublished data), to account for the stochastic variability with which harvest is likely to affect the population. The importance of the initial size of the population for its long-term persistence was examined by modelling possible trends of the population with a harvest of 600 ± 100 chicks per year with sequentially decreasing initial populations of 6,000, 5,000, 4,000 and 2,000 individuals.

The effects of habitat destruction or degradation

The consequences of habitat loss or disruption were investigated by modelling possible responses of the population to a decrease in the most immediate limiting factor, i.e. the number of available nest sites (Beissinger and Bucher 1992b, Munn 1992). Three possible scenarios of habitat availability were modelled: 1. the current situation where 30% of the island is still covered by primary forest and 70% by secondary (4,553 ± 1,821 nests); 2. where secondary forest has extended to 83% of the island and the remaining 17% is left protected to comply with the target set by the Convention on Biological Diversity (CBD), which established protection goals of terrestrial and inland water areas by 2020 (i.e. 3,570 ± 1,498 nests (Millennium Ecosystem Assessment 2005); and, 3. where all suitable habitat has been cleared apart from an untouched/protected (primary forest) area equivalent to 17% of the island (i.e. 1,674 ± 606 nests).

Consequences of harvest vs. habitat loss

The effects of harvest quotas on Grey Parrot population trends are likely to depend on the way these quotas are managed and implemented. In some countries, harvest pressure has been highly variable through the years owing to continuous changes in the relevant legislation and the effectiveness of its enforcement (UNEP-WCMC 2014). The effects of this variability were explored against those of a fix yearly quota. A simulation was run both for a variable quota of 900 ± 603 (i.e. SD = 67% as for exports declared by Cameroon, the major exporter of Grey Parrots between 1981 and 2013) and for a fixed harvest quota of exactly 900 chicks.

Finally, the interaction between changes in harvest pressure and the reduction of suitable habitat was tested by simulating the effects of three levels of annual harvest pressure (i.e. 600 ± 100, 900 ± 100 and 1,200 ± 100), with three degrees of habitat

degradation (i.e. with a maximum of 5,000, 3,000 and 1,000 available nest sites) for the next 40 years. Each simulation was run for three different harvesting technique scenarios: 1. *chick harvesting,* where only chicks are taken from nests as was the tradition in Príncipe (Juste 1996; Melo 1998); 2. *nest raiding,* where one adult is taken every two chicks as a simulation of the removal of a parent at the moment of nest raiding (e.g. in Ghana; Dändliker 1992); and 3. *indiscriminate trapping*, where individuals are taken randomly from the population, for example the trapping at clay licks in Cameroon; Ngenyi 2002, 2003).

5.4 Results

Model validation

The model was made to approximately fit the known trend of the population between 1995 and 2014 (Fig. 2). During the years of harvest, Príncipe's population underwent a steeper decline than predicted by the model, but after the implementation of the trade ban it experienced a steady recovery.
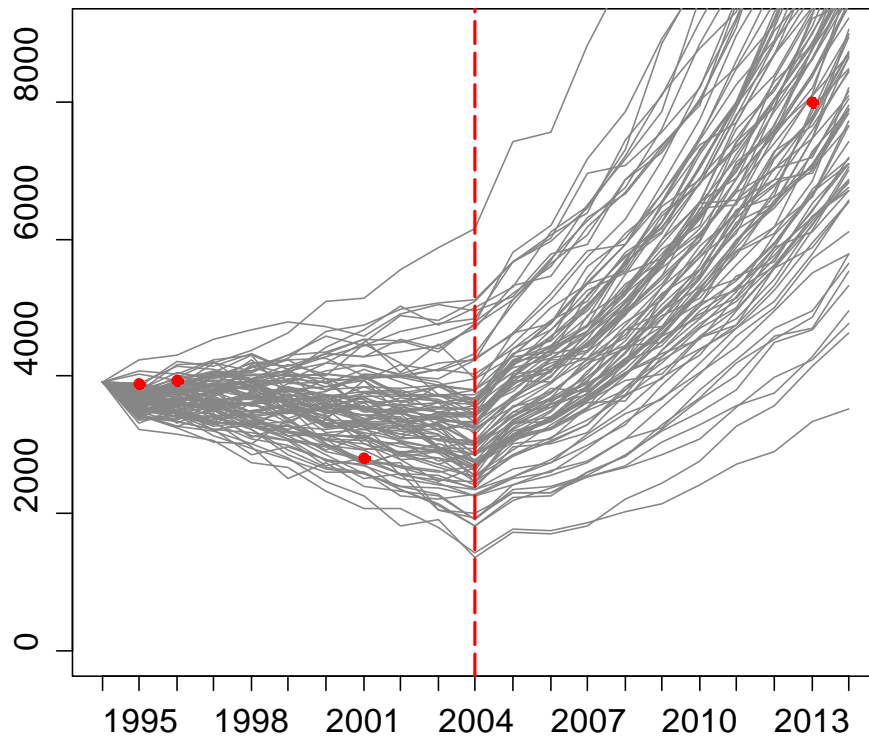
Figure 5.2. Partial validation of the model through the simulation for the 1995–2014 period, for which the Grey Parrot population trajectory is known. Red dots are estimates of population size for the years 1997, 1998, 2003 and 2014 based on distance sampling and flyway counts (§ 3.4.4). Harvest pressure was set to 600 ± 100 chicks for the first 10 years (i.e. until the ban enforced in 2005 marked with a red dashed line).

Grey Parrot population dynamics

Under current conditions, the population is predicted to continue its growth for the next 50 years with no constraints apart from the number of nest sites, which would set a carrying capacity of about 100,000 individuals (Fig. 3).
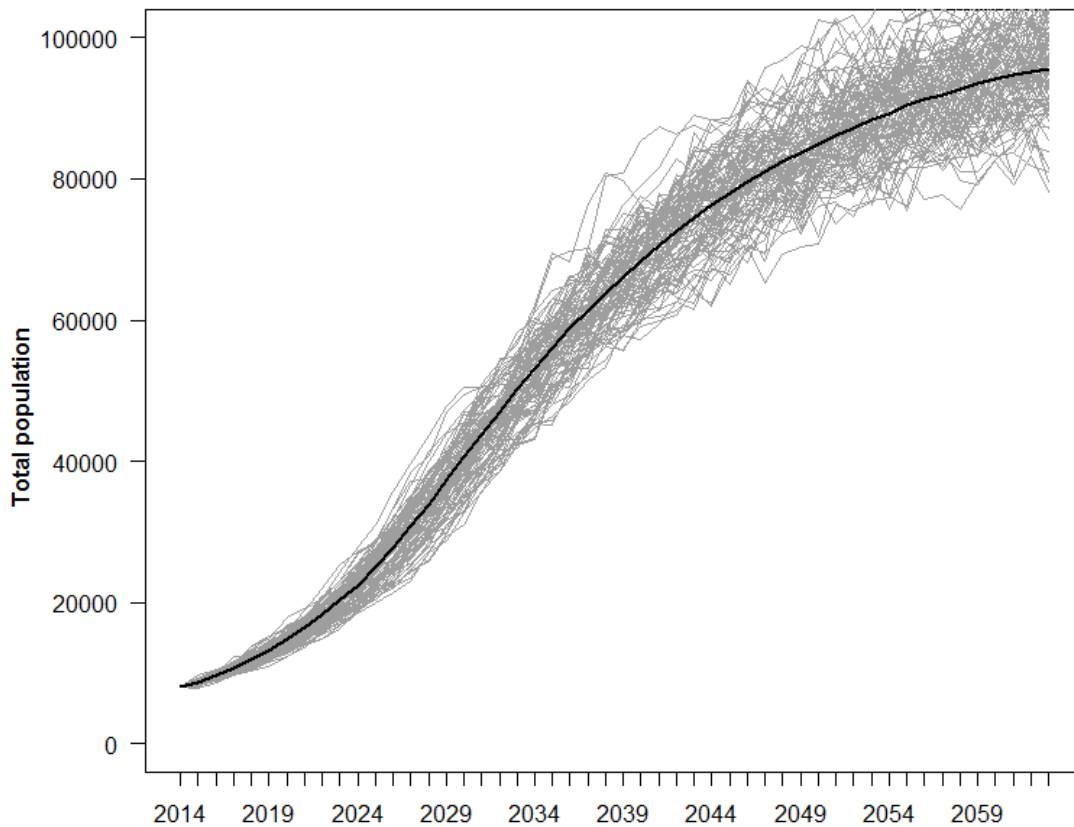
Figure 5.3. Predicted trend for Grey Parrot population on Príncipe in the next 50 years without any harvest pressure or habitat change, i.e. 42.6% primary and 57% secondary (5,502 ± 2,136 nests).

The Grey Parrot population shows a different sensitivity to the variation of some key demographic parameters. A 30% decrease in juvenile survivorship (from 52% to 22%) would cause a significant restraint on population growth, and once juvenile survivorship drops under 15%, the population is likely to disappear in 50 years (Fig. 4). The population is around three times more sensitive to a change in adult survivorship, and a decrease of just 12% is likely to compromise its survival (Fig. 5). There is a strong resilience to a possible reduction in nest success, as a drop of 45% would still have a non-significant impact on the long-term persistence of the population (Fig. 6).
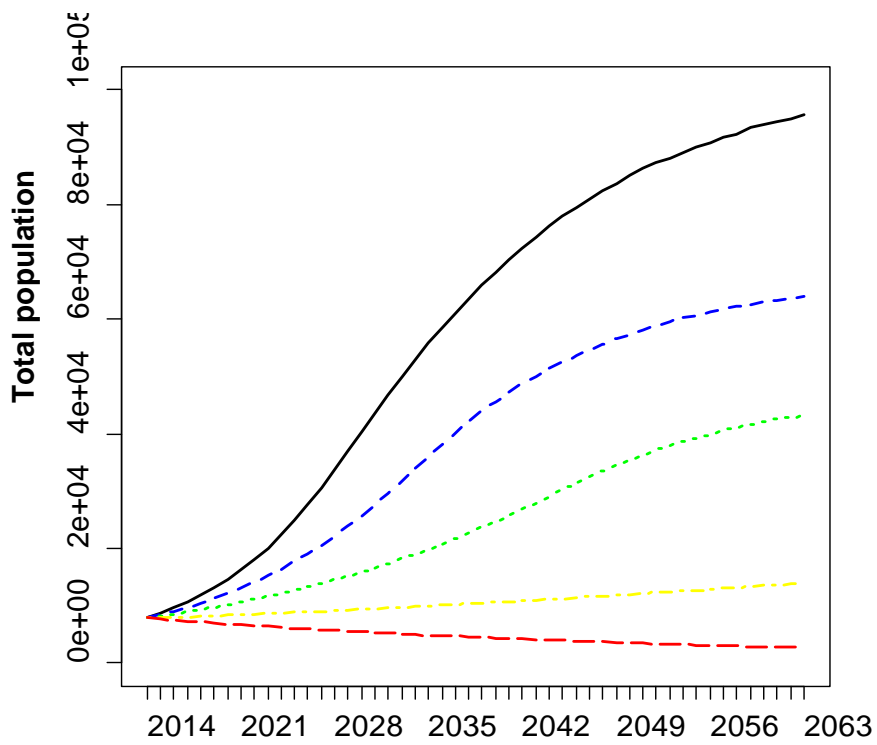
Figure 5.4. Sensitivity of population trend to decrease juvenile survivorship (solid black = 52%, dashed blue = 42%, dotted green = 32%, dot-dashed yellow = 22%, long-dashed red = 12%).
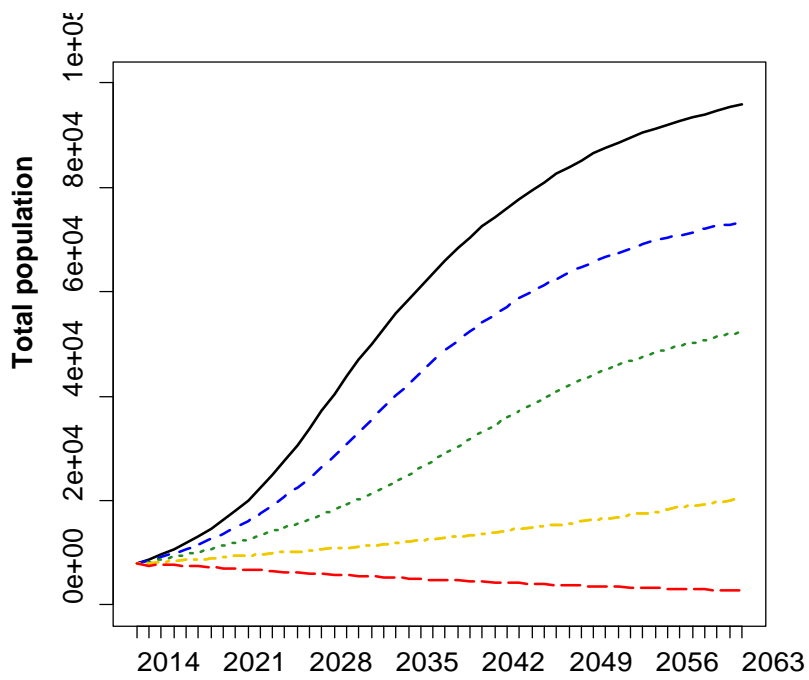
Figure 5.5. Sensitivity of population trend to decrease in subadult and adult survivorship (solid black = 91%, dashed blue = 88%, dotted green = 85%, dot-dashed yellow = 82%, long-dashed red = 79%).
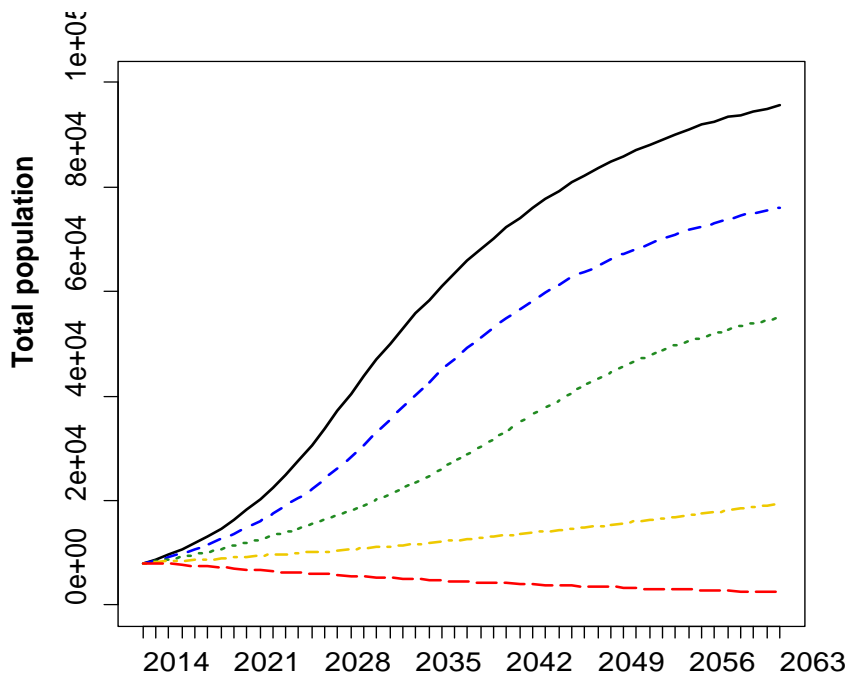
Figure 5.6. Sensitivity of population trend to decrease in nest success (solid black = 77%, dashed blue = 62%, dotted green = 47%, dot-dashed yellow = 32%, long-dashed red = 17%).

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Response to harvest pressure

When subject to a continuous harvest of chicks, under the existing environmental circumstances, the population growth is unaffected at least up to a quota of 900 ± 100 individuals per year (Fig. 7a-c). Any constant harvest exceeding the 1,000 chicks per year is progressively more likely to be rapidly inverting the population trend and driving it to extinction (Fig.7d).
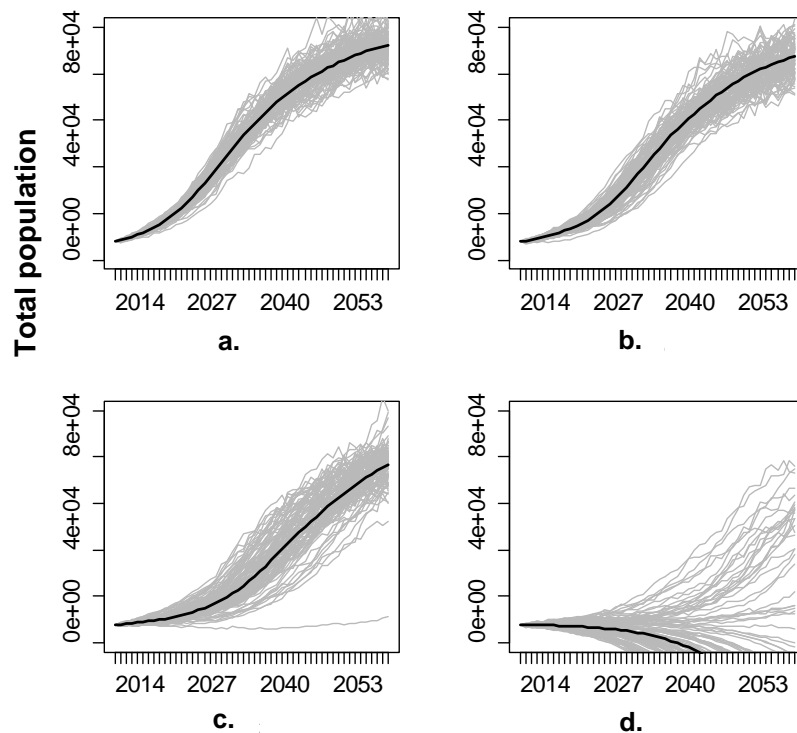
Figure 5.7. Predicted population trend in response to an annual harvest of a. 300 ± 50, b. 600 ± 100, c. 900 ± 100, d. 1,200 ± 100 chicks.

The effects of harvest are inversely proportional to the size of the starting population. At mean harvests of 600 ± 100 chicks per year, decreasing the starting population from 6,000 to 4,000 individuals changes the predicted long-term trend significantly from a steady growth towards carrying capacity to a decline to extinction within an average of 37 years (Fig. 8).
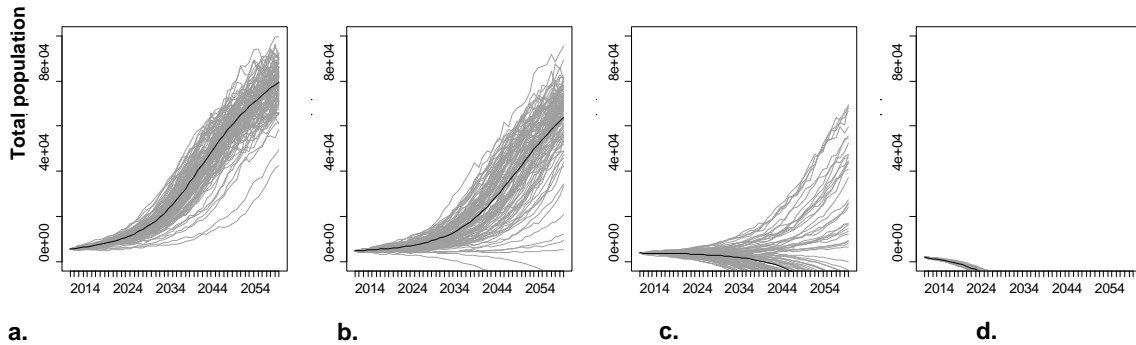
Figure 5.8. Predicted trends of the population with an annual harvest of 600 ± 100 chicks per year with an initial population of a. 6,000, b. 5,000, c. 4,000, and d. 2,000 individuals.

The medium- to long-term impact of harvest varies also with way that the quota is implemented. The same yield of 900 chicks per year may not affect sustainability of the population if implemented as a fixed quota (Fig. 9a). However, if the same 900 chicks are taken at a highly variable rate in different years, as happened in Cameroon between 1981 and 2013, there is a much greater probability that the population may decline. The differences in the mean effect is produced because in the variable harvest the benefits of the lower-than-average numbers of chicks taken in some years are dampened by the effect of the limited nest availability (Fig. 9b).
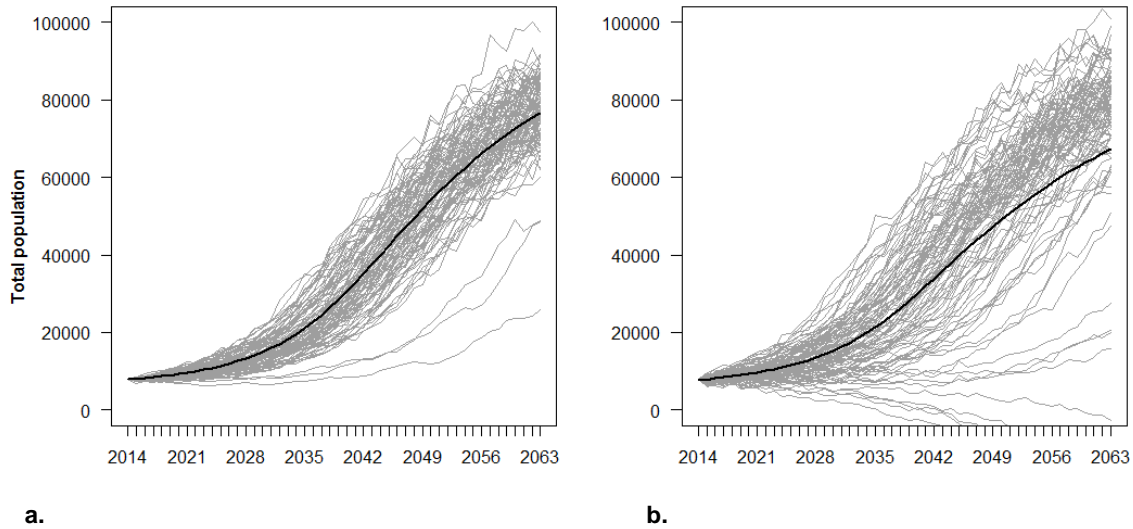
Figure 5.9. Difference between harvesting a. a fixed quota of 900 chicks each year, and b. a mean ± SD 900 ± 603 i.e. the variability of Grey Parrot exports from Cameroon between 1981 and 2013.

The effects of habitat destruction or degradation

If subject only to an incremental degradation or habitat loss, the population's maximum size is likely to decrease progressively as the number of nest sites decreases. In the extreme scenario, where all the island's forest is cleared except for the 17% protected portion, the population would not easily exceed 30,000 individuals (less than a third of its potential on the island in the current conditions; Fig. 10C).
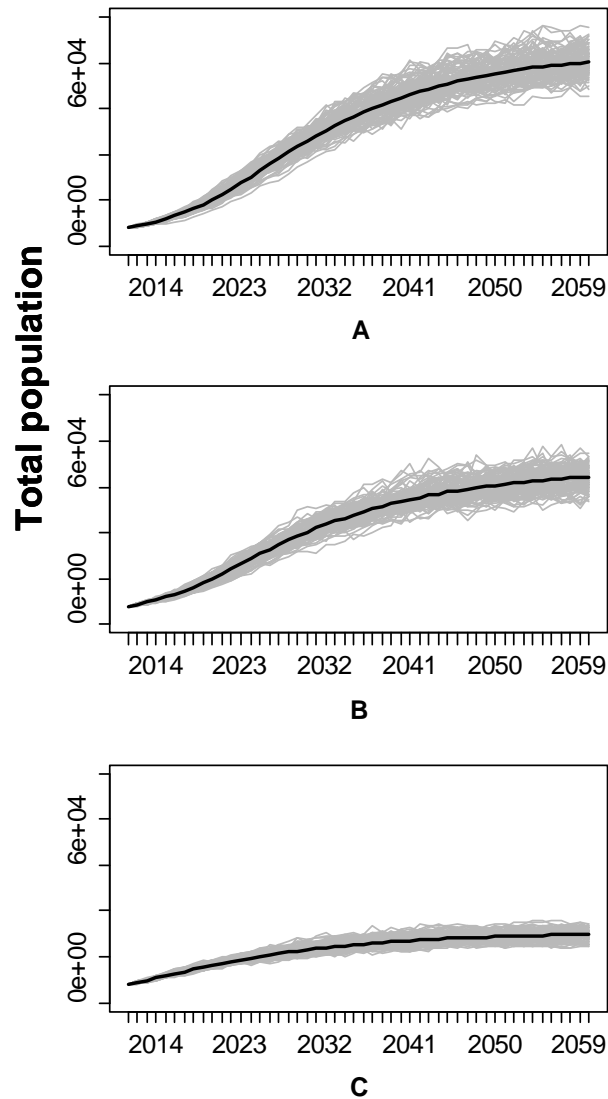
Figure 5.10. Possible scenarios of habitat change under A. 30% primary and 70% secondary forest (i.e. 4,553 ± 1,821 nests), B. 17% and 83% (i.e. 3,570 ± 1,498 nests), and C. only 17% primary (i.e. 1,674 ± 606 nests).

Effects of concurrent harvest and habitat loss

The growth of the population is not threatened by low levels of harvest, no matter the technique used (proportions of juveniles/adults taken). Growth, however, is rapidly

slowed and eventually halted by a reduction in habitat quality. On the other hand, if exposed to a heavier harvest (i.e. ≥ 900 chicks per year), unless only chicks are harvested and a good number of nest sites are available, the population would suffer an inevitable decline to extinction. The timescale of such a decline can vary from 15 to more than 40 years (Table 4). Finally, beyond a certain magnitude, harvest is never sustainable, and the population is destined to die out within 30 years. Overall, taking of chicks from nests was the least deleterious harvest technique.

Table 5.43. Predicted time to extinction for different magnitudes of harvest, yielded with a variety of techniques (chick harvesting = chicks only, nest raiding = one adult every two chicks, and indiscriminate trapping = random), in a range of scenarios with different habitat quality (i.e. maximum number of nest sites available).

Max no. nests	Quota	Chicks only	2 chicks : 1 adult	Random
5,000	600 ± 100	-	-	-
	900 ± 100	-	-	> 40
	1,200 ± 100	29	14	13
3,000	600 ± 100	-	-	-
	900 ± 100	-	> 40	39
	1,200 ± 100	29	14	13
1,000	600 ± 100	-	40	32
	900 ± 100	31	16	15
	1,200 ± 100	16	10	11
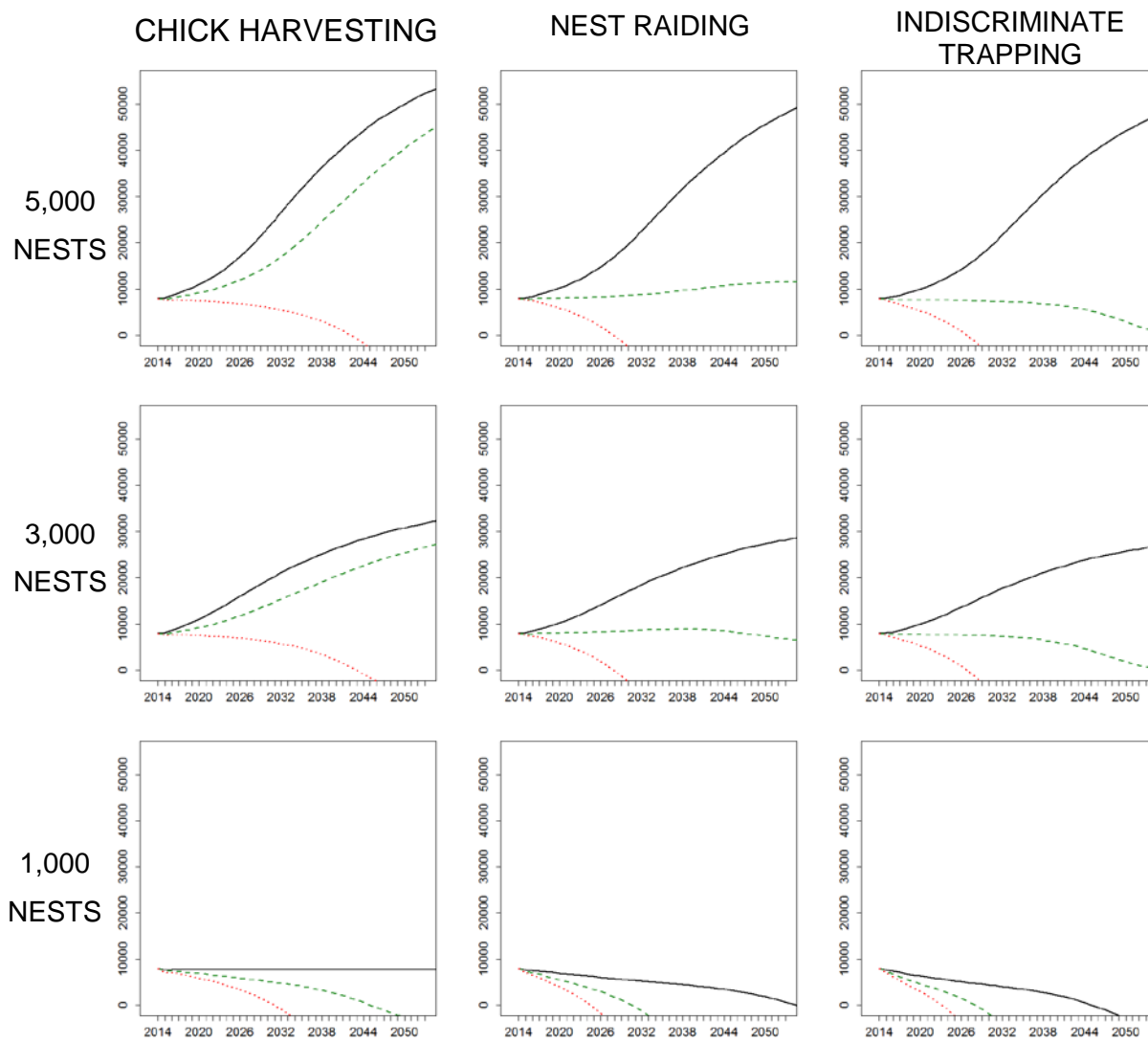
Figure 5.11. Predicted 40 year trends when the population is subject to different magnitude of harvest (solid black = 600 ± 100, dashed green = 900 ± 100, dotted red = 1,200 ± 100), yielded with a variety of techniques (chick harvesting, nest raiding and indiscriminate trapping), in a range of hypothetical scenarios with decreasing habitat quality (i.e. maximum number of nests = 5,000, 3,000 and 1,000).

5.5   Discussion

Grey Parrot in Príncipe

The Grey Parrot population on Príncipe is healthy and growing at a steady pace. Retrospective PVA modelling showed that this is part of a rapid recovery from the slow decline the species suffered during the years of intense harvest. This change of course coincides with the putting in place of a regional ban on trade. It is likely that, without the new legislation on trade, the decline would have resulted in the eventual disappearance of the species from the island or possibly just limited its population size. Nonetheless, even in the latter case, an extremely small and isolated population may have been then exposed to a heightened risk of extinction owing to inbreeding depression and increased vulnerability to natural catastrophes (Gilpin 1996, Juniper 2002). In a small area like Príncipe it is very likely that the ban on trade has catalysed the population recovery, although it may be difficult to demonstrate the link incontrovertibly (Cooney and Jepson 2006), since other environmental factors may have had played an important role. The island offers some particularly favourable conditions for Grey Parrots, namely a forest cover which allows a high density of nest sites (see Chapter 4), the absence of any natural predators or likely competitors for tree cavities or food (Jones and Tye 2006) and some inaccessible and untouched areas of primary forest (Exell 1973). Nonetheless, the results draw attention to the high recovery potential of the population, despite its isolation (i.e. absence of immigration), provided suitable environmental conditions are yet available and anthropogenic pressures are sufficiently controlled. This may bring hope for Grey Parrot populations in those countries where human impact is relatively dilute (e.g. Cameroon), whereas a similar recovery would be very unlikely in other areas (e.g. Ghana), where there are too many adverse concurrent anthropogenic factors e.g. logging, farming and general reduction of habitat quality (Annorbah et al. submitted). Although PVAs are normally developed to predict future population trends or extinction risk (Beissinger and McCullough 2002), the validation of the model through the historical information available from Príncipe is an example of how PVA models

may be used retrospectively to analyse past cases of population decline or extinction to better understand the relative contributions that several threats may have made.

Population dynamics

According to the model, the population in Príncipe has the potential to become very large in the next 50 years. The island has, already, exceptionally high densities compared to the rest of its range, as well as compared to parrot species elsewhere (Marsden and Royle 2015; see Chapter 2). Nonetheless, it is likely that some currently unknown density-dependent mechanism would affect the population before it reaches such high densities. Among these competition for a suitable variety of food resources would be the next most likely factor to affect the population, followed by other factors such as change in social behaviour and heightened exposure and vulnerability to diseases. More importantly, these results can be interpreted as an, albeit imprecise, indication of the species' recovery potential from low densities, which is an important parameter for the prioritization of conservation effort, since PVAs are most usefully applied to small, and possibly declining, populations (Master 1991, Beissinger 2002, Mills and Lindberg 2002). Sensitivity analysis identified adult survivorship as a key a parameter for the long-term persistence of the populations, more so than juvenile survivorship or nest success. This is not surprising given the biology of the species which, as other large parrot species (and other large tropical species e.g. see Dolman et al. 2015), has small clutch size and a long period of parental care (Benson et al. 1988), a slow sexual maturation (Lantermann 2000), and a long lifespan (Young et al. 2012). In most long-lived species, such as parrots, seabirds and geese, adults (i.e. the reproductive potential of the population) have usually evolved a high survivorship as a mechanism of fitness optimization (i.e. by weighing current reproductive benefits against cost of future reproduction; Linden and Møller 1989). More importantly, this highlights the utility of PVA models for predicting potential responses by the studied population. A good understanding of the relative importance of different demographic parameters in the population dynamics of a given species is key to its conservation management (Caughley and

Sinclair 1994, Hilborn et al. 1995). In particular, quantifying the importance of survivorship of different age classes in the long-term persistence of populations is the ecological basis of any sustainable harvesting (Pöysä 2004).

Response to harvest pressure

The Grey Parrot population in Príncipe has been exploited with no formal regulation for many years (Juste 1996), and, despite evidence of a decline, it has managed to retain a relatively large population with a strong recovery potential. One of the reasons may lie in the harvest technique traditionally adopted on the island, where chicks are harvested annually from a number of known cavities, the locations of which are passed on from generation to generation (Melo 1998). This strategy leaves untouched a proportion of unknown nest cavities (likely those in inaccessible areas but also ones which are simply not found) to function as a reservoir for recruitment (Wilson et al. 1994, Hanski 1998). Furthermore, harvest of just chicks is equivalent to a reduction in juvenile survival, a form of mortality of which, owing to the species' life history, the population is relatively tolerant (see '*Population dynamics*' above). The modelling of different harvest scenarios seems to corroborate this theory showing how the long-term trend population is relatively unperturbed by a constant harvest of a moderate number of chicks. Beissinger & Bucher (1992) came to similar conclusions through the implementation of harvest models on other parrot species.

These results have to be interpreted with caution, as sustainability of chick harvest is strictly dependent on at least three factors. First, the magnitude of the yield is crucial, and even a relatively small increase in harvest 'quota' (e.g. beyond 900 individuals per year) can seriously alter its sustainability. Second, the initial size of the population is likely to make a difference between persistence and extinction: small populations tend to lack the reproductive potential to cope with a constant harvest (Gurtin and Murphy 1981), although this may result in extinction only in the long term (20–30 years), running the risk that the threat goes undetected (see '*Consequences of harvest vs. habitat loss*' below). Third, sustainability of harvest might depend on annual variability in numbers harvested. In some of the major exporting countries

(e.g. Cameroon and DRC) changes in the legislation and significant deficiencies in effectiveness of enforcement cause 'quotas' to fluctuate greatly from year to year (UNEP-WCMC 2014), which can increase the impact of the harvest. This variability is far from being the much-needed 'optimal threshold strategy', where quotas are periodically reviewed and revised to optimise yield and minimise the risk of depleting the resource (Lande et al. 1997). Thus, one of the main hindrances to the implementation of sustainable quotas for Grey Parrots in Africa, and for other parrot species elsewhere (see Beissinger and Bucher 1992b), is the lack of suitable legislation and sufficient resources to enforce it (CITES 2013). It has been questioned that, even where sustainable harvest programmes could be implemented, these may not be economically viable, as they would have to compete with captive breeding facilities and illegal trade (Beissinger and Bucher 1992a). Although costs associated to *in situ* sustained harvest may be much lower than those of *ex situ* breeding centres (Clubb 1992), large investments in law enforcement would be needed to control and outcompete the lucrative illegal market (Lewis et al. 1990, Pires 2012). This is part of an ongoing debate which concerns many valuable species, and it has been argued that restrictions, or even bans, that are not adequately regulated can even encourage wildlife trade instead of deterring it (Rivalan et al. 2007).

The influence of habitat loss/degradation

In many cases, habitat loss is likely to affect the availability of nests more than it does the availability of food (Newton 1994, Newton 1998). Many parrot species are known to be adaptable to different food resources (Renton 2001), and this has allowed some species to successfully spread their range into urban areas (Lowry and Lill 2008, Davis et al. 2012). The availability of nesting sites is known to be a limiting factor for parrots (Beissinger and Bucher 1992b). In hole-nesting species, tree cavities are often the limiting resource (Newton 1994), and since these occur with greater frequency in larger trees, the effects of less invasive types of exploitation such as selective logging may be comparable to those of total deforestation (Cockle

et al. 2010). Simulations certainly show that habitat loss and/or disruption gradually limits the carrying capacity of the population, consistent with what has been found in other studies (Beissinger and Bucher 1992b, Munn 1992). Nonetheless, once again, results from PVA model simulations should be taken with caution as deforestation may have further concurrent and interacting effects which are harder to detect, and which may exacerbate the severity of the threat (Didham et al. 2007). The simulation of a bad-case scenario, where only a small proportion of habitat is preserved, suggests that reduced areas of forest (e.g. protected areas), may still hold small but healthy populations, and thus act as refugia for the species, although a drop in accessibility to a variety of food resources (e.g. in secondary forest and plantations) are bound to affect the population. This also shows a notable ability to survive in small patches of suitable forest, and thus a certain resilience to fragmentation. Thanks to their high mobility, parrots are known to inhabit successfully habitats characterised by high levels of fragmentation (Bonadie and Bacon 2000, Nunes and Galetti 2007).

Effects of concurrent harvest and habitat loss

In most cases, harvest is acting concurrently with habitat loss, making the evaluation of its effects more difficult (e.g. Ghana; Annorbah et al. submitted). Moreover, parrots are taken from the wild with a range of techniques which will differ in their impact on the population. A limited harvest from a healthy population living in a good habitat can be sustainable irrespective of the technique employed. However, the increase of the quota by just a few hundred individuals may drive the population to extinction (see '*Response to harvest pressure*' above). Populations were found to be particularly sensitive to harvest of adults. These findings are consistent with theoretical predictions for populations experiencing density-independent mortality mainly restricted to juveniles (Linden and Møller 1989), and applies to many long-lived species from parrots (Beissinger and Westphal 1998), to other bird species (e.g. albatrosses; Weimerskirch 1992), to reptiles (e.g. Congdon et al. 1994) to mammals (e.g. Taylor et al. 1987). The decrease of habitat quality concurrently with constant

harvest dampens the population's growth, leading it to a slow but inevitable decline. Extinction debt or delayed extinction (Tilman et al. 1994) happens when a populations' mortality slightly exceeds productivity, ultimately causing extinction, but only after several generations (Jackson and Sax 2010). The phenomenon has been documented among several tropical bird species in the face of rapid deforestation (Brooks et al. 1999, Szabo et al. 2011), and in parrots is enhanced by the slow population turnover (Koleff and Gaston 2001). A major benefit of PVA models is their potential for predicting these long-term declines, which may otherwise be overlooked by short-term ecological fieldwork (Beissinger 2002). Despite operating concurrently, harvest and habitat loss affect the population at different levels, where the former acts directly on extrinsic mortality, and the latter on carrying capacity. Understanding the mechanism by which multiple threats act differently on the population is crucial to both identify and tackle those threats with greater effectiveness (Evans et al. 2011).

Model limitations

PVA models are a simplification of reality, and the precision and accuracy of their output is always proportional to the quality of the data with which they have been built (Boyce 1992). Furthermore, the more the model is tailored to include the species' peculiar biological characteristics the more accurate its predictions will be (Beissinger and Westphal 1998). The simplicity of the model developed for Príncipe (e.g. no interspecific competition, or immigration or emigration) was an advantage for isolating the effects of some intrinsic and extrinsic factors, but, on the other hand, it would need to be restructured to be applied to another population (e.g. Akçakaya 2000). Ultimately, the usefulness of a model depends largely on the explicit evaluation of the assumptions used to build it (Coulson et al. 2001). There are also a number of unknown or unmeasurable parameters that cannot be included into a model. For example sociality has been implicated in the extended lifespans of some taxa (Carey and Judge 2001), and the social nature of most parrots has been shown to affect extrinsic mortality in less favourable environments (Munshi-South et al. 2006). Moreover, in a situation of isolation like Príncipe, shortage in food availability

may affect stress levels and in turn reflect on individual fitness as has been shown in other parrot species (Stoleson and Beissinger 1997, Masello and Quillfeldt 2004). Finally, despite the debate on the reliability of their results, there is an emerging consensus that PVAs are a useful tool for predicting population trends with reasonable degree of precision, where high-quality data on demographic parameters are available (Brook et al. 2000, Brook et al. 2002).

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5.7 Appendix I.

R script for the building and implementation of the PVA model to simulate the Grey Parrot population trajectory for the 1995–2014 period.

```
#Load required packages
library(quadprog)
library(popbio)
library(mvtnorm)
library(msm)

# SETTING FIXED MODEL PARAMETERS

lambda <- (8388/2822)^(1/9)
  # lambda = initial estimation of population increase i.e. #
  9th root of (N in 2012 / N in 2003)

nsimul <- 1000
# Number of simulations to be run

nyears <- 20
# Number of years to run the model for

T1 <- 1
# duration of age class 1 (juvenile) in years

T2 <- 2
# duration of age class 2 (sub-adult) in years

T3 <- 42
# duration of age class 3 (adult) in years
# i.e. maximum life span = 45

female.ratio <- 0.46
# ratio of females born per brood

harvestm <- 600
# mean number of chicks harvested each year

harvestSD <- 100
```

```
#SD of number of chicks harvested each year

nest.success <- 0.77
# nest success

Fmean <- 1.96
# Mean number of chicks per brood

Fsd <- 0.1
# SD number of chicks per brood

  # MATRIX PARAMETERS ARE PRESENTED FOR CLARITY(formulas as #
  in § 5.3.1)ALTHOUGH SOME WILL BE INCLUDED IN THE        #
  SIMULATION SCRIPT IN ORDER TO BE RECALCULATED IN EACH   #
  SIMULATION

p1 <- s1*(1 - (((((s1/lambda)^T1) - ((s1/lambda)^(T1-1))) /
(((s1/lambda)^T1)-1)))
  # probability of juveniles of surviving and remaining in #
  the same stage

p2 <- s2*(1 - (((((s2/lambda)^T2) - ((s2/lambda)^(T2-1))) /
(((s2/lambda)^T2)-1)))
  # probability of sub-adults of surviving and remaining in #
  the same stage

p3 <- s3*(1 - (((((s3/lambda)^T3) - ((s3/lambda)^(T3-1))) /
(((s3/lambda)^T3)-1)))
  # probability of adults of surviving and remaining in the  #
  same stage

F <- (round((rtnorm(mean=1.96,sd=0.72,n=1,lower=1, upper=3)),
digits = 0)) * female.ratio
  # Reproductive output per brood calculated from the mean #
  and SD, rounded to the nearest integer, with a minimum # of 1
  and a maximum of 3, multiplied by the ratio of    # females


f2 <- 0
# fecundity of individuals in sub-adult stage

f3 <- (F*p3)  * nest.success
```

```
  # fecundity of individuals in adult stage multiplied by nest
  # success rate

g1 <- s1 * (((s1/lambda)^T1) - ((s1/lambda)^(T1-1))) /
(((s1/lambda)^T1)-1))
  # probability of juveniles of surviving and growing into the
  # sub-adults

g2 <- s2 * (((s2/lambda)^T2) - ((s2/lambda)^(T2-1))) /
(((s2/lambda)^T2)-1))
  # probability of sub-adults of surviving and growing into  #
  the adults

g3 <- 0
  # probability of adults of surviving and growing into a    #
  further age class (which in does not exist)

N1 <-  662
# initial number of individuals in juvenile stage

N2 <-  1324

# initial no. of individuals in sub-adult stage

N3 <- 1692

# initial no. of individuals in adult stage


pop <- matrix(c(p1,f2,f3,g1, p2,0,0, g2, p3), nrow=3, ncol=3,
byrow=F)

  # creates the populatation matrix (called 'pop') with the
  demographic above parameters


  # CREATE THE POPULATION VECTOR (i.e. initial population
  # estimate for the 3  age classes)

N <- matrix(NA,nrow=nyears, ncol=3)
```

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```
  #creates an empty matrix with 3 columns and as many rows # as
  the years of simulation


N[1,] <- c(N1,N2,N3)

  #replaces the first row (i.e. year one) with the initial #
  estimate of the population for the 3 age classes



Ntot <- matrix(ncol=nsimul,nrow=nyears)

  # creates an empty matrix where total population figures  #
  from each simulation will be stored

  # All of the above is included in a series of loops that #
  will simulate the demographic process



for(j in 1:nsimul) {
  # runs a 'j' loop for the previously established number of #
  reiterations



for (i in 1:10){
# runs a first 'I' loop for 10 years (i.e. till 2005
# when the trade ban has been put in place)

  #  All  parameters  are  recalculated  in  each  year  of
  # simulation

s1 <-  (round((rtnorm(mean=0.52,sd=.08,n=1)), digits = 2))

s2 <- (round((rtnorm(mean=0.91,sd=.03,n=1)), digits = 2))

s3 <- (round((rtnorm(mean=0.91,sd=.03,n=1)), digits = 2))


p1  <-  s1*(1  -  ((((s1/lambda)^T1)  -  ((s1/lambda)^(T1-1)))  /
(((s1/lambda)^T1)-1)))
```

```
p2 <- s2*(1 - (((( s2/lambda)^T2) - ((s2/lambda)^(T2-1))) /
((( s2/lambda)^T2)-1)))


p3 <- s3*(1 - (((( s3/lambda)^T3) - ((s3/lambda)^(T3-1))) /
((( s3/lambda)^T3)-1)))


g1 <- s1 * (((( s1/lambda)^T1) - ((s1/lambda)^(T1-1))) /
((( s1/lambda)^T1)-1))


g2 <- s2 * (((( s2/lambda)^T2) - ((s2/lambda)^(T2-1))) /
((( s2/lambda)^T2)-1))



harvest<-       (round((rtnorm(mean=harvestm,sd=harvestSD,n=1)),
digits = 0)) * female.ratio
```
 # harvest is calculated each time from mean and SD set #
at the beginning and rounded to the nearest integer # and
multiplied by the ratio of females

```
F<-(round((rtnorm(mean=fmean,sd=fsd,n=1,lower=1,     upper=3)),
digits = 0)) * female.ratio
```

 # Setting number of nest sites as a limiting factor

```
limit<- N[i,3]
```
 # For each simulation selects the number of adults
 # breeding…

```
limit[limit>2280] = 2280
```
 # … and sets a maximum from the maximum number of nest #
sites (see § 5.3.2)

```
x<- N[i,3]
```
 # Again for each simulation selects the number of adults
 # breeding

```
logcurve <- function(x) {F*(1-((x/2280)^10))}
```
 # logcurve is the theta-logistic curve which describes #
nest availability

```
area <- integrate (logcurve, lower = 0, upper = limit)
```

```
        # Integration of the above function between 0 and
        # 'limit' (i.e. number of breeders but not more than
        # maximum number of nests…

FK <-(area$value)/x
        # … and findng the mean 'adjusted fecundity' value
        dividing by the number of # breeders

f3 <- (FK*p3)    * nest.success

        #for each simulation f3 is calculated from the mean
        #'adjusted fecundity' value

pop <- matrix(c(p1,f2,f3,g1, p2,0,0, g2, p3), nrow=3, ncol=3,
byrow=F)


trade <- matrix(NA,nrow=1, ncol=3)
        # creates a an empty vector called 'trade' where to     #
        store number of birds to be harvested for each of the #
        three age classes


trade[1,] <- c(harvest,0,0)
        # 600 individuals are set to be harvested from age class
        # 1 i.e. juveniles


N[i+1,]<-(N[i,] %*%pop)- trade
        # multiplies each row of the N matrix the population   #
        matrix, then detracts the number of harvested birds # for
        from the relevant age class, and stores the            #
        results the next row of the same matrix

Ntot[i+1,j]<-sum(N[i+1,])
        # calculates the total population from each simulation #
        and stores them in Ntot

}

        # end for first 'i' loop
```

```
for (i in 11:(nyears-1)){
    # runs a second 'i' loop for the remaining years (i.e. #
    from 2005 onwards). Same as previous loop but with no #
    harvest.

s1 <- (round((rtnorm(mean=0.52,sd=.08,n=1)), digits = 2))

s2 <- (round((rtnorm(mean=0.91,sd=.03,n=1)), digits = 2))

s3 <- (round((rtnorm(mean=0.91,sd=.03,n=1)), digits = 2))


p1 <- s1*(1 - ((((s1/lambda)^T1) - ((s1/lambda)^(T1-1))) /
(((s1/lambda)^T1)-1)))

p2 <- s2*(1 - ((((s2/lambda)^T2) - ((s2/lambda)^(T2-1))) /
(((s2/lambda)^T2)-1)))

p3 <- s3*(1 - ((((s3/lambda)^T3) - ((s3/lambda)^(T3-1))) /
(((s3/lambda)^T3)-1)))

g1 <- s1 * ((((s1/lambda)^T1) - ((s1/lambda)^(T1-1))) /
(((s1/lambda)^T1)-1))

g2 <- s2 * ((((s2/lambda)^T2) - ((s2/lambda)^(T2-1))) /
(((s2/lambda)^T2)-1))

F <- (round((rtnorm(mean=fmean,sd=fsd,n=1,lower=1, upper=3)),
digits = 0)) * female.ratio

limit<- N[i,3]

limit[limit>2280]  = 2280

x<- N[i,3]

logcurve <- function(x) {F*(1-((x/2280)^10))}

area <- integrate (logcurve, lower = 0, upper = limit)

FK <-(area$value)/x
```

```
f3 <- (FK*p3)   * nest.success

pop <- matrix(c(p1,f2,f3,g1, p2,0,0, g2, p3), nrow=3, ncol=3,
byrow=F)

N[i+1,]<-(N[i,] %*%pop)


Ntot[i+1,j]<-sum(N[i+1,])

}
     # end of the second 'I' loop

Ntot[1,j]<-sum(N[1,])

}
     # end of 'j' loop



     # PLOT TOTAL POPULATION TRAJECTORIES

plot(((Ntot[,1])/0.46), xaxt = "n", type = "l", lwd = 1, lty =
1, xlab = expression(bold( "C")),
     ylab = "", ylim = c(0,100000), col="grey72")

for (i in 2:100){

lines(((Ntot[,i])/0.46),  type  =  "l",  lwd  =  1,  lty  =  1,
col="grey72")

}

     # plots the results of each of the 1,000 simulations
     # through a loop. The x axis is purposefully blanked
     # (se below)

axis(1, at=1:20, labels=c(1995:2014))
     # labels on x axis

TREND<-rowMeans(Ntot)
```

180

```
     # calculates the mean of totals from each simulation    #
     for each given year i.e. mean trend of all population #
     trajectories

lines((TREND/0.46), type = "l", lwd = 2, lty = 1)
     # plots the mean trend

mtext("Total  population",  side=2,  outer=T,  at=0.5,  cex=1,
font=2)
     # adds relevant labels to the x axis
```

Appendix II. Information of parrot nest failur in the wild, available in the literature

Species	% Nest failure (harvest)	% Nest failure (natural causes)	Total nest success	Tot nest years	Reference
Cape parrot *Poicephalus robustus*	0	22	78	9	C. Downs *in* Pain et al. 2006 Wirminghaus et al. 2002
Grey-headed parrot *Poicephalus fuscicollis suahelicus*	0	25	75	1	C. Symes *in* Pain et al. 2006
Ruppell's parrot *Poicephalus rueppellii*	0	42	58	12	Selman et al. 2000
Citron-crested cockatoo *Cacatua sulphurea citrinocristata*	0	87.5	12.5	8	Walker et al. 2005
Echo parakeet *Psittacula eques*	0	75	25	12	Jones and Swinnerton 1997
New Caledonian parakeet *Cyanoramphus saisetti*	0	25	75	8	J. Theuerkauf, S. Rouys *in* Pain et al. 2006
Philippine cockatoo *Cacatua haematuropygia*	0	31	69	51	P. Widmann, I.D. Widmann, M. Boussekey, S. H. Diaz *in* Pain et al. 2006
Glossy black cockatoo *Calyptorhynchus lathami halmaturinus*	0	62	38	118	Garnett et al.1999 S. Garnett *in* Pain et al. 2006
Golden shouldered parrot *Psephotus chrysopterygius*	0	68	32	800	S. Garnett *in* Pain et al. 2006
White-tailed black cockatoo *Calyptorhynchus f. latirostris*	0	39	61	543	Saunders 1982
Palm cockatoos *Probosciger aterrimus*	0	78	22	41	Murphy et al. 2003
Eclectus parrot *Eclectus roratus*	0	73	27	146	Heinsohn and Legge 2003
Red-necked Amazon *Amazona arausiaca*	0	0	100	6	S. Koenig *in* Wright et al. 2001
Yellow-billed Amazon *Amazona collaria*	0	37	63	8	S. Koenig *in* Wright et al. 2001
St. Lucia Amazon *Amazona veriscolor*	0	17	83	38	J. Gilardi *in* Wright et al. 2001
Puerto Rican Amazon *Amazona vittata*	0	13	87	38	F. Vilella *in* Wright et al. 2001
Green-rumped Parrotlet *Forpus passerinus*	0	57	43	36	S. Stoleson, S. Beissinger *in* Wright et al. 2001
Monk Parakeet *Myiopsitta monachus*	0	68	32	17	J. Eberhard *in* Wright et al. 2001
Major Mitchell cockatoo *Cacatua leadbeateri*	1	14	85	89	Rowley and Chapman 1991

Species						Source
Black-billed Amazon *Amazona agilis*	2	45	53	59		S. Koenig *in* Wright et al. 2001
Lilac-crowned Amazon *Amazona finschi*	7	57	36	28		K. Renton *in* Wright et al. 2001
Vasa parrot *Coracopsis vasa*	9	53	38	32		J. Ekstrom *in* Pain et al. 2006
Blue-headed Parrot *Pionus menstruus*	10	5	85	8		A. Soza-Asanza *in* Wright et al. 2001
Green-cheeked Amazon *Amazona viridigenalis (Puerto Rico)*	12	0	88	5		J. Meyers *in* Wright et al. 2001
Cuban Amazon *Amazona leucocephala*	17	4	79	2862		V. Berovides-A., X. Gálvez-A., J. Wiley *in* Wright et al. 2001
Uvea parakeet *Eunymphicus cornutus uvaeensis*	18	46	36	22		P. Primot, M. Saoumoé *in* Pain et al. 2006
Yellow-shouldered Amazon *Amazona barbadensis*	22	18	60	296		A. Trujillo, F. Rojas-Suárez, V. Sanz, M. Albornoz, A. Rodríguez-Ferraro *in* Wright et al. 2001
Green-cheeked Amazon *Amazona viridigenalis (Mexico)*	32	17	51	145		E. Enkerlin-Hoeflich, J. Gonzalez-Elizondo *in* Perez and Eguiarte 1989
Yellow-naped Amazon *Amazona auropalliata (Costa Rica)*	37	5	58	37		T. Wright *in* Wright et al. 2001
Yellow-cheeked Amazon *Amazona autumalis*	39	22	39	176		E. Enkerlin-Hoeflich, J. Gonzalez-Elizondo *in* Perez and Eguiarte 1989
Yellow-headed Amazon *Amazona oratrix*	41	15	44	57		E. Enkerlin-Hoeflich, J. Gonzalez-Elizondo *in* Perez and Eguiarte 1989
Grey parrot *Psittacus erithacus*	42	33	25	12		Tamungang 1997
Orange-winged Amazon *Amazona amazonica*	44	22	34	15		A. Sosa-Asanza *in* Wright et al. 2001
Hispanolan Amazon *Amazona ventralis*	46	9	45	156		F. Vilella *in* Wright et al. 2001
Red-tailed Amazon *Amazona brasiliensis*	49	13	38	78		P. Martuscelli *in* Wright et al. 2001
Yellow-naped Amazon *Amazona auropalliata (Guatemala)*	73	14	13	68		A. Brice, K. Joyner, C. Toft, J. Wiley *in* Wright et al. 2001
Yellow-crowned Amazon *Amazona ochrocephala*	77	14	9	21		A. Rodríguez *in* Wright et al. 2001
Red Shining Parrot *Prosopeia tabuensis*	79	21	0	19		Rinke 1989
White-faced Amazon *Amazona kawalli*	88	4	8	25		P. Martuscelli *in* Wright et al. 2001
Vinaceous Amazon *Amazona vinacea*	88	6	6	25		P. Martuscelli *in* Wright et al. 2001
Grey parrot *Psittacus erithacus*	100	0	0	38		McGowan 2001
Grey-headed parrot *Poicephalus fuscicollis suahelicus*	100	0	0	1		C. Symes *in* Pain et al. 2006
Blue-Throated Macaw *Ara glaucogularis*	-	55	-	31		Berkunsky et al. 2014

Chapter 6. Conclusions and suggestions for future research

6.1   Conclusions

The goal of this PhD was to investigate the ecology of the Grey Parrots *Psittacus erithacus*, to learn about the species' basic population dynamics and better understand the mechanism by which the harvest for the international pet trade and habitat loss may affect the species. The island of Príncipe was chosen as a study area owing to its healthy Grey Parrot population, its long tradition of parrot harvest and the disturbed-to-pristine range of habitats which covers the island.

Chapter 2 estimated population densities and the total population size for the island both in the pre- and post-breeding seasons. It investigated habitat associations and identified the most important environmental factors behind some extraordinarily high densities, namely nest-tree species in the pre-breeding, and slope and food-tree species in the post-breeding season. Despite being a large and mobile population over a relatively small area, Grey Parrots proved to have marked habitat preferences and it was highlighted how these vary significantly in the two surveyed seasons. A better understanding of seasonal habitat use is key to the conservation of the species and suggests how preserving a matrix of habitats will be essential. Moreover, the findings have implications for the way surveys should be designed, since the density or population estimates resulting from them may suffer from significant bias if their timing is not chosen wisely.

Chapter 3 focused on the methods available to conservation scientists to estimate parrot densities and ultimately population sizes. Although distance sampling methods are currently the preferred, and arguably the most accurate, survey methods, these are often not an option owing to a lack of local expertise, time or resources. Thus, three simple and inexpensive methods were tested as

possible alternatives. Encounter rates were shown to be workable proxy for actual parrot densities, and may prove of great utility where other more precise methods cannot be used. Long watches proved to be far less accurate and precise: this method may be useful only in a few cases where vantage points offer optimal visibility over small areas, and can provide a high number of encounters. Finally, the count of individuals along habitual flyways were found to be a possible good method to monitor some populations over time, although further testing is required. The chapter underlies how there is major scope for research in similar straightforward and low-cost survey techniques as conservation in resource-poor areas would benefit greatly from them.

Chapter 4 investigated the breeding biology of Grey Parrots, focusing on their nesting habitat requirements and how these might affect productivity. Unsurprisingly, the best nest site opportunities are offered by large ageing trees, which is where natural cavities have more chance to appear. None of the habitat characteristics measured seems to affect productivity strongly, suggesting that other factors (e.g. characteristics of the hollows, parental experience) may be more important. The study looked also at the spatial distribution of nests and revealed exceptionally high nest densities, leading to a discussion as to why this is not the case elsewhere in their distribution range. This chapter also provides a better understanding on how nest site availability may or not be a limiting factor for breeding densities in Príncipe.

Chapter 5 assembled all the information from the previous sections, as well the best data available on Grey Parrots (or similar parrot species to fill occasional gaps), to build a PVA model and to better understand the species' population dynamics in the face of harvest and habitat loss, both in Príncipe and elsewhere. The model was developed to reflect as closely as possible the biological and ecological characteristics of the species. The model gave an insight into the historical trajectory of the population in Príncipe under the effects of harvest first and a ban on trade later, underlying the usefulness of these models in the retrospective analysis of past declines or extinctions. The population was predicted to increase in the near future, showing a strong potential of the species for a rapid recovery, given that some favourable

conditions still apply. No data were available on the carrying capacity of the island, or on the possible consequences of other density-dependent processes (e.g. competition for food resources). Nonetheless analyses were mainly focused on those more realistic cases in which populations are small or declining. A look at the species' population dynamics identified adult mortality as the most crucial among the demographic parameters, owing to biological characteristics typical of a long-lived species. Harvest was shown to be sustainable only with small quotas and where a number of limiting conditions apply, while the major effect of habitat disruption and loss was in lowering the predicted maximum size of the population. Nonetheless, since these factors often act concurrently their effects can be much more unpredictable. Harvest appears to be the major threat, particularly when this is poorly regulated and implemented with techniques that include the harvesting of adults. Harvest in combination with habitat loss may result in long extinction lags which could be overlooked by conservation ecologists. The usefulness of PVA models as a tool of investigation is highlighted.

6.2   The future of Grey Parrots in Príncipe

Despite a long tradition of intense chick harvest (Juste 1996, Melo 1998), the Grey Parrot population in Príncipe shows all the signs of a healthy volume and trajectory, with population and nest densities greater than those ever recorded for the species elsewhere. The island appears to hold particularly favourable conditions for the species, and the recent ban on harvest has most likely facilitated a steady growth. The island has seen minimal commercial exploitation in the last 20 years, and many of the old plantations have been rapidly recolonized by secondary forest (Figueiredo et al. 2011). Nonetheless, a retrospective PVA revealed how, despite the ideal conditions, before 2005 Grey Parrots may have been slowly but steadily declining to a very small, and thus vulnerable, population. Grey Parrots have always played an important role in the local traditions of the island, being kept as pets in local households, and appearing in the coat of arms on the island's flag. Parrot trade has allowed a

handful of people to settle economically (e.g. set up a business, build a house) on the island, although there is no evidence that the benefits have spread far beyond those directly involved in the business (Melo 1998; S. Valle unpublished data) . Despite being the independent promoters of a ban on trade through a regional legislation in 2005, local authorities have recently been showing strong interest in resuming the trade, as soon there is evidence that it might be safe to do so. Since 2012, a small number of Grey Parrots have been illegally traded for the local or international market (50 birds maximum; S.Valle unpublished data). This trafficking seems to be favoured by the lack of controls, and linked to the presence of a new wave of possible buyers (i.e. expatriates associated with a recent influx of investments for tourism development). Owing to its large population and favourable environmental conditions, Príncipe could theoretically be used to refine the parameters for a sustainable harvest of Grey Parrots. However, local authorities lack the political will, the economic resources and the technical skills which would be necessary to regularly monitor the parrot population, control the trade, and persecute illegal activities. Moreover the investment needed to implement a sustainable harvest schemes may greatly exceed the revenue resulting from the trade. Social and political factors, have been shown to be a major hindrance to such schemes for other species of parrots as well (Beissinger and Bucher 1992).

6.3   What are the major threats to Grey Parrot populations?

Grey Parrot populations are threatened by a combination of mutually interacting effects from harvest and habitat loss. However, these operate in different ways on the population (see chapter 5). Harvest directly affects overall extrinsic mortality, and this is particularly detrimental when, owing to the technique used, a certain proportion of adults is taken. On the other hand, habitat degradation or loss will limit the carrying capacity of a population, so that a healthy population may still be in place but its size, and thus its capacity to cope with other threats, will be much lower. Understanding the mechanisms by which threats affect

parrot populations is key to an effective prioritization of conservation effort (Brook et al. 2000).

Habitat destruction and loss in tropical Africa is a complex problem which involves ecological, political and economic aspects (Barnes 1990). It ultimately finds its roots in a fast-growing human population vying for resources in the same areas which hold high levels of biodiversity (Balmford et al. 2001). For a long time, the traditional approach to the preservation of these habitats was to set aside areas for nature conservation (i.e. protected areas), but this is no longer viable as available surface is running out (Musters et al. 2000). Thus, there has been a call to pursue a different strategy, and search for trade-off solutions which may benefit both local development and biodiversity (i.e. community-based approach) (Sinclair et al. 2000, du Toit et al. 2004, Robinson 2006). Grey Parrots have been shown to be adaptable to a number of different habitats and food resources (Benson et al. 1988), and likely benefit from a landscape matrix more (see chapter 2; Marsden and Pilgrim 2003), which is compatible with certain types of habitat disturbance. In some extreme cases, the species is known to live in small self-sustaining populations in urbanised environment, e.g. in Kampala, Uganda, and Kinshasa, DRC (Martin et al. 2014), and Accra, Ghana (N. Annorbah unpublished data). Much more limiting may be the availability of suitable nest sites (see chapter 4), which sets conservationists some specific priorities for the preservation of the species.

6.4   Can Grey Parrot harvests be sustainable?

Harvest has a major impact on Grey Parrots and many other parrot species, as, from a population prospective, it increases the population's extrinsic mortality for the yielded age class (Beissinger and Bucher 1992). The impact on the population can, theoretically, be negligible if only juveniles are targeted and a number of conditions apply: 1. the initial population is abundant and healthy (see chapter 3 and 5); 2. only a small number is taken yearly (see chapter 5); 3. habitat destruction and loss are not concurrently affecting the population (see chapter 4 and 5); 4. enough knowledge on population structure and status is

generated, and resources are available for its periodical update; and 5. resources are available for the implementation and strict enforcement of the harvest scheme. It is almost impossible to find anywhere within the Grey Parrots' range where all these conditions apply, as populations in many countries are already on the brink of extinction (e.g. Côte d'Ivoire, see chapter 3; Ghana, Annorbah et al. submitted). Moreover, no matter how precise predictions from population models can be, they are still imperfect simulations of reality, as social and political, as well as overlooked ecological factors, may impede the implementation of sustainable harvesting (Beissinger and Bucher 1992, Beissinger 2001).

Nevertheless, Grey Parrots are currently listed by CITES in Appendix II, i.e. a species that is not necessarily threatened with extinction, but may become so unless trade is subject to strict regulation in order to avoid extinction of the species in the wild (CITES 2015). Thus the species is legally harvested and traded by some countries despite there being minimal understanding of its population status and dynamics (Martin et al. 2014). Quotas are often established on poor-quality data and the enforcement of the relevant legislation is patchy and insufficient (CITES 2013). A review of the number of wild-caught Grey Parrots declared to be imported and exported internationally in the last 30 years reveal a number of incongruences (i.e. they don't add up; UNEP-WCM 2014), which reflects how flawed management of the trade is, and how this may offer numerous opportunities for the illegal trade to persist (Pires 2012). Many have advocated an international ban on wild parrots trade as the only means of preserving psittacines (e.g. WPT 2004, Gilardi 2006) , but this approach has been challenged and is still the object of debate (Cooney and Jepson 2006, Rivalan et al. 2007, Challender et al. 2014). Whereas it is CITES' and national governments' responsibility to promulgate suitable legislation and enforce them, conservation ecologists can focus on producing the necessary quality evidence for them to make informed decisions. Particularly in Africa, where resources available often are scarce, there is great scope for the development of easy and inexpensive methods (e.g. survey and modelling) which could potentially provide data on a range of important biological aspects (e.g. nest density, productivity). This information, ultimately, may curb the current drift towards an

unregulated trade and, in the long term, support a revision of the current legislation.

6.5   Lessons learned and directions for future research

The Grey Parrot is highly charismatic and a threatened species (BirdLife International 2014), and yet very little is known of its ecology, population trends and conservation status (Martin et al. 2014). The main cause lies in the fact that the species, as most parrots, is very hard to study, even in a small area like Príncipe. They are canopy-dwellers, hard to detect when perched and highly mobile (Collar 1998). Their beaks can destroy most methods of individual marking, and yet the few techniques that may withstand their strength (e.g. wing-tags) are likely to strongly affect their survival (Saunders 1988, Meyers 1994). Grey Parrots are impossible to age after the first year and even this is very hard to do in the field (Dändliker 1992). They can rapidly move through large stretches of forest which, in most cases, are remote and /or of difficult access (Martin et al. 2014). The nests are difficult to find and to monitor because they are often located more than 20 metres high in trees (Dändliker 1992, Amuno et al. 2010). This makes nesting density almost impossible to calculate. As in other parrot species, life history traits are extremely hard to collect, and this is the first study to build a demographic model of Grey Parrots, resorting to the best data available on the species on Príncipe, and elsewhere. Each chapter of this thesis represents a step forward in the understanding of Grey Parrot's ecology and population dynamics, and there is much potential for further research. However, as the species is declining rapidly and the resources available are limited, research efforts need to be prioritised. Two main areas of investigation stand out from this thesis: 1. the need for practical, inexpensive, yet reliably accurate survey methods; and 2. the use of PVA models as a tool for exploring population sensitivity to different threats and provide useful indications for management purposes.

The first obstacle to Grey Parrot conservation, as with that of other parrot species, is often the lack of the most basic information on the wild populations,

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namely densities, sizes and trends (Marsden and Royle 2015). This information is essential for the development of coherent conservation and management plans for any species (Primack 1993, Newson et al. 2008), and it constitutes the foundation of the IUCN Red List scheme (Lamoreux et al. 2003, IUCN 2014). The most accurate density estimation methods are always desirable, but these need specific skills, abundant resources and long time, none of which are often available, particularly in the tropics. Thus, there is major scope for scientists to devise and test alternative low-cost methods which can help local conservation practitioners to estimate and monitor populations. Unmanned remote devices like audio recorders have been used to surveying parrots South America (Haselmayer and Quinn 2000, Figueira et al. 2015), although this requires a considerable investment in equipment. A more flexible, and relatively quick and easy, alternative would be to explore further the use of occupancy modelling as a general surrogate for estimates of parrot abundance (MacKenzie et al. 2002, MacKenzie et al. 2005). This thesis tested three possible methods and succeeded in finding a correlation between actual densities and encounter rates. Although results from chapter 3 are encouraging, further investigation would be welcome in looking at counts along habitual flyways as a possible survey method. Similarly, might counts along rivers or in claylicks be used to monitor parrot populations? Is photo-trapping a possible way of surveying Grey Parrots in clearings in the forests of Central Africa? Is there a relationship between other existent databases (e.g. national bird atlases or birdwatching) evidence and actual parrot/bird densities? Each of these methods, or a combination of them, may be key to the estimation, and thus, the conservation, of one or more species, as the goal would be to find, in each situation, the best trade-off method between precision and practicability.

The second main investigation area was the use of PVAs a research tool to inform conservation management. There is a great potential in developing further the model proposed in chapter 5 to improve its precision in predicting trends in Príncipe and, more importantly, to undertake similar analysis of Grey Parrot populations on the mainland Africa. There is also scope to use the same model as a basis to develop PVAs for other parrot species. There is great interest in this aspect, as it would help prioritizing conservation efforts as well as

providing useful information for the regulation of harvesting activities (CITES 2013). The use of PVAs has been long debated (Coulson et al. 2001), but there seem to be general consensus in its potential accuracy and usefulness if results are taken with due care (Brook et al. 2000, Reed et al. 2002). Significant investment is needed in the building of an accurate model (Beissinger and Westphal 1998), and the collection of suitable life history data would need to be a priority. Nonetheless, PVAs have also the potential of simulating an endless array of possible scenarios, and may well be the key method to gather those much sought-for 'non-detriment findings' which ought to be at the base of sustainable exploitation of all species (CITES 2015). Scientists need to provide and validate quality of demographic data, but the development of pre-packaged software (e.g. Vortex and Ramas) makes the simulation of possible scenarios accessible to most conservation practitioners (Lacy 1993). In the case of harvested species, such as parrots, the resulting figures cannot be taken as true predictions, and it would not be advisable to use them to establish quotas. Nonetheless, these may be an important and useful indication of when harvest is not an option (e.g. very small populations, disturbed or unsuitable habitat) and when further research is advisable to quantify sustainable quotas.

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