Factors affecting the life history, abundance and distribution of the yellow-shouldered Amazon parrot (*Amazona barbadensis*) on Bonaire, Netherlands Antilles

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ABSTRACT

Understanding the factors that limit endangered populations is a foundation of ecological study and conservation management. Many parrot species are vulnerable to extinction, but despite their threatened status and familiarity there have been few studies of parrots in the field. Over three years I observed the life history, abundance and distribution of the yellow-shouldered Amazon parrot (*Amazona barbadensis*) on the island of Bonaire. Data were first compared to other *A. barbadensis* populations and other *Amazona* species, and then examined in relation to a suite of biotic and abiotic factors in order to understand the factors constraining population growth. Reproductive success was generally lower on Bonaire than in other *A. barbadensis* populations, but was typical of the genus. Different measures of productivity were influenced by specific factors. Female parrots laid larger clutches where the availability of food resources on two spatial scales was greater. Hatchability was low compared to other bird species, probably reflecting inbreeding depression. Brood size at fledging was lower in areas with high abundances of potential competitors and where introduced predators were present. Chick asymptotic weight was lowest in nests exposed to the weather. The distribution of *A. barbadensis* varied spatially and temporally across Bonaire. Parrots were more abundant in areas of mature habitat and where there were fewer potential competitors. Seasonal migrations between rural and urban areas correlated with the previous month's rainfall. *A. barbadensis* uses a wide range of rock and tree cavities for nesting and key cavity characteristics for nest site selection were identified. Apparently suitable, unused cavities are available in various habitat types but gaps in our knowledge of parrot nest selection make it difficult to conclusively assess nest site limitation. These findings indicate that a range of factors negatively affect *A. barbadensis* on Bonaire. Fortunately these issues can be resolved with conservation management strategies and a proposal for future conservation is included in this thesis.

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Chapter I

INTRODUCTION

1.1. LIMITING FACTORS AND CONSERVATION BIOLOGY

All organisms are influenced by biotic and abiotic factors in their environment. Acting through density dependent or independent processes these factors regulate or control populations (Sinclair, 1990; Johnson & Seip, 2008). This, often complex, array of factors will define patterns of survival and reproduction for individuals, and shape the abundance and distribution of species (Norris, 1993; Martin, 1995; Newton, 1998; Verhulst & Nilsson, 2008). Understanding such patterns forms the basis of ecological study and is essential for conservation.

Human beings are having a profound effect on planet earth and driving a dramatic loss of biodiversity (Pimm et al., 1995; MEA, 2005). Currently, the pattern of limiting factors experienced by a population is almost certainly influenced, ultimately, by humans. The scale of these impacts may range from overhunting of one particular species through to global climate change (Thomas et al., 2004; Sekercioglu, 2006; Thuiller et al., 2008). The discipline of conservation biology uses ecological theory to understand threatened natural systems in order to prevent extinctions (Caro, 1998). This research is valuable, when applied, because it can provide the basis for practical conservation management.

A foundation in ecology and a first step in conservation biology is an understanding of a species' basic life history (Varley et al., 1973; Jones, 2005; Townsend et al., 2005). These variables are essential for the development of population models, which may be used to inform conservation management decisions (Beissinger, 2002). The importance of understanding life history is highlighted by the now classic study of loggerhead turtles (*Caretta caretta*; Crouse et al., 1987). This population model showed that despite monumental efforts to increase productivity, the greatest increase in population size would be achieved by improving the survival of later life stages, particularly large juveniles.

Unfortunately, simply recording life history variables in order to determine population dynamics can be extremely difficult for long-lived species with slow life histories (Beissinger, 2002; Clark & Martin, 2007). Protecting the vulnerable life stages may be even harder and across a wide range of taxa it has been shown that those species with relatively slow life histories are particularly vulnerable to decline (Bennett & Owens, 1997; Cardillo et al., 2005; Clark & Martin, 2007).

Population dynamics are shaped by survival and reproduction, which in turn are influenced by a variety of biotic and abitoic factors. The range and complex combinations of different factors that may influence populations has led to a diversity of theoretical and experimental studies examining, for example, resource limitation (Cody, 1974; Pinkowski, 1976; Nilsson, 1984; Martin, 1987; Brawn & Balda, 1988; Gustafsson, 1988; Crawford et al., 2007; Robb et al., 2008), predation (Ricklefs, 1969; Skutch, 1985; Eggers et al., 2006) and environmental conditions (Connell, 1961; Schweiger et al., 2008; Ritchie et al., 2009). The successful conservation of several endangered species on Mauritius has shown that an informed, multi-faceted and pragmatic approach to the management of limiting factors can have dramatic results (Butchart et al., 2006). Food limitation was countered with supplementary feeding, nest site limitation with the provision of boxes and predators through predator control. Management even included mitigation of environmental effects on nest sites (Jones, 2005)

The same factors that determine the life history of a species can influence its spatial and temporal abundance, and distribution. The selective pressures on survival and reproduction in different environments guide an individual's decisions and lead to patterns of resource use and thus distribution (Southwood, 1977; Boyce & McDonald, 1999). Individuals will seldom inhabit areas where, for example, food is limited, there is a high a predation risk, or the environment is unsuitable for them (Connell, 1961; Cameron, 2006; Eggers et al., 2006; Chalfoun & Martin, 2007; Ritchie et al., 2009). Therefore, patterns of abundance across an environment should reflect the suitability of available habitats, in the broadest sense.

Habitat selection theory predicts that individuals distribute themselves in order to obtain the best resources available, given the constraints of competition (Fretwell & Lucas, 1969; Parker & Sutherland, 1986; Morris, 2003). Resource limitation is a fundamental problem in conservation, particularly on islands where population sizes are relatively small (MacArthur & Wilson, 1967). Understanding the factors that shape a species' abundance and distribution and their resource requirements is extremely useful for conservation biology. By using such information, biologists can predict patterns of species distribution in response to future changes, and conservation managers can resolve issues of limiting resources and distribution (Newton, 1994; Gaston, 2003; Jones, 2005; Chalfoun & Martin, 2007; Ritchie et al., 2009).

1.2. LIMITING FACTORS AND PARROTS

The parrots (Psittacidae) are a worthy if somewhat difficult group in which to investigate the factors limiting populations. They are one of the most endangered bird families, with approximately one third of the *c.*360 species classed by the IUCN as near threatened or at a greater risk of extinction (IUCN, 2008). In the genus *Amazona* there are 31 recognised species, which are distributed through South and Central America and on several Caribbean islands (Juniper & Parr, 2003). Of these, 16 (52%) are threatened to some degree with extinction, 12 (39%) of which are found in the Caribbean (IUCN, 2008).

Despite their endangered status and familiarity, little research has been conducted on wild parrots and biologists have largely ignored captive parrots. Many wild parrot species are found in remote and challenging environments where they may be all but invisible in the rainforest canopy, so it is not surprising these species are relatively under-studied. The majority of early parrot research focused on the highly visible cockatoos in the Australian wheat-belt, some of which had large or even growing populations (Smith & Saunders, 1986; Smith, 1991). More recently there has been number of studies on the genus *Amazona* which have reported the life history traits of widely distributed continental species (Enkerlin-Hoeflich, 1995; Seixas & Mourao, 2002), endangered continental species (Martuscelli, 1995; Waugh, 2006; Salinas-Melgoza & Renton, 2007) and endangered island endemics (Koenig, 2001; Beissinger et al., 2008).

Few research projects on wild parrots have been established long enough to estimate life spans and it is aviculturalists that demonstrated how long-lived parrots can be (Snyder et al., 1987; Rowley, 1990; Rowley & Chapman, 1991; Smith & Rowley, 1995; Brouwer et al., 2000; Forshaw, 2006). The combination of being long-lived and having slow life histories, places the majority of parrots in the unfortunate position where adult survival is likely to be the most important, but also the most challenging, demographic trait to measure or manage (Snyder et al., 1987; Saunders, 1990).

Many parrot species experience unpredictable environments and ephemeral food resources (Renton, 2002; Beissinger et al., 2008). They are also subject to predation, competition, and disease (Snyder et al., 1994; Heinsohn et al., 2003; Raso et al., 2006). Critically, parrots are subject to extensive human predation in the form of poaching, as well as anthropogenic loss or modification of habitat (Saunders, 1977; Wright et al., 2001; Pain et al., 2006). While a small number of studies have examined specific limiting factors, few have simultaneously considered the relative importance of various biotic and abiotic factors (Snyder et al., 1987; Beissinger et al., 2008). Similarly while there are a few published studies that have investigated parrot population biology (Smith & Rowley, 1995; Drechsler, 1998; Renton, 2001; Karubian et al., 2005; Salinas-Melgoza & Renton, 2005; Manning et al., 2007), only one has looked at multiple biotic and abiotic factors influencing parrot distribution (Drechsler, 1998).

Parrots are secondary cavity users and some parrot populations are suspected to be nest-site limited (Munn, 1992; Heinsohn et al., 2003; Sanz et al., 2003). However, there has been little research conduced on the extent of suitable but unused cavities (Lanning & Shiflett, 1983; Enkerlin-Hoeflich, 1995; Legge et al., 2004). Furthermore although cavities have been described in several studies worldwide (Nelson & Morris, 1994; Rodriguez-Estrella et al., 1995; Marsden & Jones, 1997; Sanz, 2006), very few have examined how nest-site dimensions may influence nest site selection (Marsden & Jones, 1997; Manning et al., 2004).

The overall lack of parrot studies is unfortunate because of their endangered status and the impact that humans have had on wild populations (Snyder et al., 2000; Wright et al., 2001; Pain et al., 2006). Research on the group is much needed so that scientific evidence can be used to inform management strategies and policy. Moreover, the conservation of parrots as flagship species can bring considerable benefits for entire ecosystems (Butler, 1992). This thesis aims to address some of these previous shortcomings.

1.3. STUDY AREA AND SPECIES

The yellow-shouldered Amazon parrot (*Amazona barbadensis*) is found in several isolated populations across the Southern Caribbean region (Figure 1.1). The disjunct distribution includes populations in costal areas of Venezuela and the Venezuelan islands of Margarita and La Blanquilla. On the island of the Netherlands Antilles, *A. barbadensis* is extirpated from Aruba, introduced to Curacao and extant on Bonaire. This study was conducted on Bonaire (288km^2) an oceanic island found between 68° 11' - 68° 25' West and 12° 1' - 12° 9' North (Figure 1.2). The distribution of *A. barbadensis* is widespread across the island but excludes the southern quarter of the island, which is largely a windswept wetland area. The average annual temperature is 28°C and the island receives low, irregular and localised rainfall. The average annual precipitation is 463mm, of which 51% falls in October, November and December. Near constant trade winds arrive from the east north-east with an average speed of 12.8 knots. Unlike the windward Caribbean islands, Bonaire seldom experiences hurricane force winds. The xerophytic vegetation is broadly characterised by a mixture of tall candle cactus and thorny hardwood trees that rarely exceed five meters in height. Across Bonaire the habitat has been dramatically degraded since European colonisation and the introduction of free ranging goats (De Freitas, 2005). Further habitat degradation results from poachers cutting access holes into tree nests to remove parrot chicks.

A. barbadensis is considered vulnerable to the threat of extinction with a total population of between 2,500 and 10,000 individuals (IUCN, 2008). The estimated population on Bonaire is 650 individuals, of which the proportion of breeders may be 21.5% in a given year (Chapter II). Like most parrots *A. barbadensis* roosts in raucous groups that on Bonaire can include several hundred individuals. Particular roosts are used faithfully although the distribution of individuals among roosts varies temporally. Breeding typically takes place between May and August, and nests are found in clusters or in isolation across the island, north of the town Kralendijk (Figure 1.2). Breeding pairs are socially monogamous and remain together over consecutive years, apparently maintaining their pair bond through the non–breeding season (Martin, 2009; pers. obs.). During the breeding season *A. barbadensis* pairs exclude other pairs from the immediate vicinity of their nest (Martin, 2009). Amazon parrots are secondary cavity nesters and

Chapter III

FACTORS AFFECTING THE PRODUCTIVITY OF AMAZONA BARBADENSIS ON BONAIRE

3.1. INTRODUCTION

Understanding the biotic and abiotic factors that affect survival and reproduction is fundamental in the study of ecology and for the long-term conservation of endangered species. The population dynamics of a species are shaped by survival and reproduction, and the relative impact of these variables on population growth depend on the life history of that species (Lack, 1966; Clark & Martin, 2007). Ecological theory and classic empirical studies highlight several key patterns that are important to consider in any study of the distribution and abundance of organisms (Crouse et al., 1987; Boutin et al., 1995; Akcakaya & Raphael, 1998; Beissinger, 2002).

First, slow-growing and long-lived species are more likely to be limited by survival than reproduction. For example, the now classic study of loggerhead turtles (*Caretta caretta*) showed that despite monumental efforts to increase productivity, the best effort towards ensuring positive population growth was to focus on the survival of later life stages, particularly large juveniles (Crouse et al., 1987). While a similar focus on productivity has kept the Puerto Rican Amazon Parrot (*Amazona vittata*) from extinction, failure to address the catastrophic reduction in adult survival resulting from food shortages following hurricanes has resulted in a population bottleneck lasting over 30 years (Beissinger et al., 2008).

Second, fast-growing and short-lived species are more likely to be limited by abiotic factors acting on productivity and recruitment. For example, population explosions of the Australian plague locust (*Chortoicetes terminifera*), which requires damp soil for reproduction, occur in years of high rainfall, while in years of little rain their numbers do not increase (Varley et al., 1973). Climate can dramaticaly influence the reproduction of many bird species. In Europe many insect eating species experience low productivity during wet summers, whereas in California significant reductions in productivity were reported for four passerine species during a recent dry summer (Newton, 1998; Bolger et al., 2005)

A common goal of species conservation is to mitigate the detrimental effects of factors limiting productivity and survival in order to increase or maintain population growth rate at values greater than zero (Mateo et al., 1998; Sanz et al., 2003). These include managing factors such as nest site limitation, introduced predators or human-caused mortality. As is clear from the examples above, research and conservation efforts tend to focus on productivity because it can be monitored more easily and may provide more tractable management solutions (Reid et al., 2004; Duca et al., 2009). However, in long-lived species, survival is typically more important but more difficult to manage than productivity (Crouse et al., 1987; Beissinger et al., 2008). Nevertheless, it may be appropriate to use intensive management to boost the reproductive rate of critically endangered species in order to compensate for poor survival (Jones, 2005).

The design and implementation of any conservation measures require prior assessment of the factors potentially limiting productivity and the demographic stages at which this occurs (Varley et al., 1973; Beissinger & Peery, 2007). Factors may be biotic or abiotic in origin, and may involve density dependent or independent processes (Lack, 1966; Newton, 1998). Direct effects of the environment (e.g. rainfall, temperature, seasons), environmental effects on food resources, predation, disease and competition all affect productivity and survival (Ricklefs, 1969; Skutch, 1985; Hudson, 1986; Krebs et al., 1986; Townsend et al., 2005). Determining the environmental factors that drive patterns of productivity and survival can also be complicated by their spatial scale or temporal variation (Reid et al., 2006; Chalfoun & Martin, 2007).

Parrots are a worthy if somewhat difficult group in which to investigate the range of limiting factors. They are one of the most at risk groups of organisms on the planet, suggesting that many have population growth rates at or below zero, and critically small population sizes (Bennett & Owens, 1997; Snyder et al., 2000; Juniper & Parr, 2003). Many of them experience unpredictable environments and ephemeral food resources (Renton, 2002; Beissinger et al., 2008), and they are subject to predation, competition, and disease (Snyder et al., 1994; Heinsohn et al., 2003; Raso et al., 2006). Critically, they are subject to extensive human predation in the form of poaching, as well as anthropogenic loss or modification of habitat (Saunders, 1977; Wright et al., 2001; Pain et al., 2006). However, they are generally long-lived and slow-growing, placing them firmly in that awkward position where adult survival is likely to be the most important demographic trait to manage but the most challenging to measure (Snyder et al., 1987; Saunders, 1990). Furthermore, they are often found in remote and challenging environments. Consequently, there are precious few detailed studies of parrot demography and productivity despite their conservation concern, thus further studies on any species is likely to be of great benefit the family as a whole.

Unfortunately a three year study is insufficient in duration to estimate adult parrot survival, thus in this study I focus on productivity as a first step to understanding the demography of the yellow-shouldered Amazon parrot (*Amazona barbadensis*). I report on variation in clutch size, brood size prior to fledging, and offspring asymptotic weight as a function of a suite of habitat characteristics. More specifically, I examine the relationship between these productivity measures and five aspects of habitat, ranging in scale from local to island-wide. The habitat factors include timing of breeding (index of early season environment), breeding density, food resource availability, possible competitors and introduced species, and nest site characteristics. These are justified for the following reasons.

The climate on Bonaire is highly seasonal and this may influence the timing of breeding, as in other dry environments where parrots have been found to modify clutch initiation according to such variations (Renton & Salinas-Melgoza, 1999; Sanz & Rodríguez-Ferraro, 2006). Parrots are highly social birds that often nest in clusters (Snyder et al., 1987; Smith, 1991; Enkerlin-Hoeflich, 1995). On Bonaire, the distance between neighbouring nests varies from less than 100m, to those that are isolated by several kilometres. In high density areas there can be groups of 4 nests within 200m. Food resources are also patchily distributed as a result of habitat degradation and highly localised rainfall. This patchiness generates spatial variation that may act directly or in combination with the distribution of potential nest sites to generate large variation in productivity. Introduced predators in island systems are a global problem and *A. barbadensis* on Bonaire is exposed to both rats and feral cats. There are also several native and introduced bird species that are potential competitors for food and nest sites. Finally, cavity nest sites are limited to suitable cliffs and trees that are patchily distributed across the island and a wide range of nest cavity dimensions is used (Chapter V), and these may influence productivity. Thus, I examine habitat use at small and large scales, defining habitat in the broadest sense as the abiotic and biotic factors that may limit productivity.

3.2. METHODS

3.2.1. STUDY AREA AND SPECIES

This study was conducted on Bonaire (288km^2), in the Southern Caribbean Sea between 68° 11' - 68° 25' West and 12° 1' - 12° 9' North. The island has an average annual temperature of 28°C and receives low, irregular and localised rainfall. The average annual precipitation is 463mm, of which 51% falls in October, November and December. Near constant trade winds arrive from the east north-east with an average speed of 12.8 knots.

A. barbadensis is a medium-sized parrot (275-365g). Like most parrots, breeding pairs are socially monogamous. Pairs remain together over consecutive years and appear to maintain their pair bond through the non-breeding season (Martin, 2009; pers. obs.). Breeding typically takes place between April and August, and nests are found across the northern half of the island. Amazon parrots are secondary cavity nesters, and on Bonaire *A. barbadensis* nests in tree and rock cavities. The latter are found either in large boulders or on cliff faces (~20m high), in either heterogeneous volcanic or limestone formations (De Freitas, 2005).

3.2.2. NEST LOCATIONS AND MONITORING

Structured nest searches were conducted with the help of volunteers each year. Nests were located by tracking pairs exhibiting nest-prospecting behaviour, or by opportunistic searches of cliffs and trees. The identity of known breeding individuals was confirmed from their ring combinations and plumage patterns where possible. Nesting pairs that bred in more than one year were nest site faithful with the exception of four pairs that moved to another cavity within ~100m of their original nest. Possible nests were inspected for activity either by eye or with digital cameras. Active nests were inspected approximately twice a week from before egg-laying (April) until fledging or failure. Once incubation commences the female remains in the nest almost constantly until the oldest chick is approximately two weeks old. To minimise disturbance at this time inspections were preferentially conducted only once the female had left the nest to be fed by the male.

3.2.3. QUESTIONS

My objective was to determine whether the productivity of *A. barbadensis* on Bonaire is affected by abiotic and biotic factors. I used three measures of productivity: clutch size, brood size prior to fledging, and chick asymptotic weight. I examined how each of these response variables was affected by five groups of explanatory variables:

1) Timing of breeding
2) Proximity to key food resource patches and other breeding pairs
3) Food resource at the nest
4) Competitor abundance and predator presence at the nest
5) Nest structural characteristics

The response and explanatory variables are described in Table 3.1. Independent variables in the food resources (3) and competitors/predators (4) analyses were generated by applying principal component analysis (PCA) to highly correlated sets of variables measured in the field (see Table 3.1. and Results below). In the food resource PCA, the first five components explain 79.65% of the variation in the original data. In the competitor/predator analysis the first four principal components describe 77.54% of the variation within the community. Axis definitions are provided in the Results section below.

Timing of breeding and proximity measures were treated together in one analysis. A second analysis focused on food availability, followed by competitors/predators in a third analysis, and nest structural characteristics in the final analysis. Thus, there are three response variables and four sets of independent variables (Table 3.1). I included clutch size as a covariate in the brood size prior to fledging analyses, and brood size (prior to fledging) as a covariate in the chick asymptotic weight analyses.

3.2.4. SAMPLE SIZES AND DATA PROCESSING

Observations were conducted on a total of 84 clutches over three breeding seasons. Pairs were observed breeding in three, two or one seasons (n = 9, 12 and 29 pairs respectively). The number of pairs observed changed each season largely because new nests were found. Any repeated measurements (<10 pairs) were averaged to give a single measure for each pair.

Table 3.1. Response and explanatory variables used to determine the factors affecting the productivity of *Amazona barbadensis* on Bonaire, Netherlands Antilles (2006-08).

	Variable	Description	Justification
Response variables			
	Clutch size	Total eggs laid	Measure of female investment
	Brood size prior to fledging	Count of chicks *c.*2 weeks before their estimated fledge date	To exclude loss from poaching, which typically occurs immediately prior to fledging
	Asymptotic mass	Maximum weight of any chick in the brood	Measure of offspring quality
Explanatory variables			
	Initiation date	Day# Jan 1st = Day 1	Affects productivity (Norris, 1993)
Proximity	Distance to food resource patch	Distance in metres measured with GPS.	Fruit trees and dense clusters of native food trees are exploited by parrots
	Distance to 2nd neighbour		Indicator for clustered nest sites
	Number of nests within 200m	Count	Measure of density
Food resource at nest	Calabash (*Crescentia cujete*)	Count of individuals over 1m tall within a 1ha quadrat centered on the nest (Northern edge 50m north of the nest)	Seeds within large fruit and flowers eaten
	Cossie (*Acacia tortuosa*)		Seeds within legume pods eaten
	Mesquite (*Prosopis juliflora*)		Seeds within legume pods eaten
	Black willow (*Capparis odoratissima*)		Seeds eaten
	Yellow wood (*Casearea tremula*)		Fruit and seeds eaten
	West Indian birch (*Bursera simaruba*)		Fruit eaten
	Kadushi – candle cactus (*Subpilocereus repandus*)		Flower, fruit and flesh eaten
	Datu - candle cactus (*Ritterocereus griseus*).		Flower, fruit and flesh eaten
Competitor abundance at nest	Brown-throated conure (*Aratinga pertinax xanthogenius*)	15minute bird count at dawn (0600 - 0900) or dusk (1600 - 1900) within a 1ha quadrat centred on the nest	Abundant endemic subspecies, only other parrot. Observed diet overlap
	Troupial (*Iterus icterus*)		Abundant and introduced; observed diet overlap
	Scaly-naped pigeon (*Patagioenas squamosa*)		Large fruit eater; observed diet overlap
	Bare-eyed pigeon (*Columba corensis*)		Large fruit eater; observed diet overlap
	White-tipped dove (*Leptorila verreauxi*)		Observed diet overlap
	Pearly-eyed thrasher (*Margarops fuscatus*)		Known nest competitor, causing mortality to eggs and chicks
Nest characteristics	Entrance height above ground	Plumb line entrance to ground, cm.	Related to incidence of nest predation in other parrots
	Exposure	Subjective measure: protec'd (1) – expo'd (3)	Accounts for multiple dimensions and exposure to the weather
	Nest entrance area	Entrance height x width cm^2	Related to predator access
	Nest floor area	Nest floor length x width cm^2	Possible constraint on brood size

3.2.5. STATISTICAL MODELLING

All data were centred at zero and normal-scaled prior to analysis. All statistical analyses were conducted in the R environment using general linear models (R Development Core Team, 2009).

I analysed the data in each of the four analysis sets using an information theoretic approach (Burnham & Anderson, 2002). This approach compares all nested candidate models under a maximum model using Akaike's Information Criterion (AIC). The Akaike values (AIC) of different models can be directly compared by their difference (Δ_i) to the best fitting model, which has the smallest AIC. Akaike weights (w_i) were also calculated for each model. The w_i is the probability that model i would be included in the final model.

Akaike weights were also calculated for each explanatory variable (k) from the confidence set. This estimates the probability that of all the variables considered, kth variable would be in the best model. As the ratio of observations (n) to k was low (all analyses) the second-order criterion AICc was used to produce likelihood-based measures of model fit.

In each analysis set, all possible subsets of each model were fitted. These permutations were then ranked from best to worse on their AICc. Model residuals from the AICc best model were visually assessed and the data transformed where appropriate and re-analysed. For each analysis the confidence set of models is reported (Appendices 1-12). This is the smallest subset of candidate models for which the Δ_i sum to 0.95. Within the confidence set the Akaike weights were recalculated to sum to 1, as recommended by Burnham and Anderson (2002). The explanatory variable selection probabilities and coefficients (β) for each explanatory variable were also recalculated from the confidence set.

The information theoretic approach works best with as few explanatory variables as possible (Whittingham et al., 2006). Specifically the number of possible model permutations (directly related to k) should not exceed the number of observations (Burnham & Anderson, 2002). Various constraints limited the data available for each analysis. Where the number of observations was low, an initial analysis was conducted in order to identify explanatory variables with low Akaike weight. This approach was necessary in order to achieve an acceptable ratio of n/*k*.

3.3. RESULTS

I report first on details of the PCA used to ordinate the food resources data and the predator/competitor data. This is followed by three sections each corresponding to one of the three dependent variable sets. In each of these sections, I report on the four analyses that each comprise a set of independent variables. The variable selection probabilities and coefficients from these analyses are shown in Table 3.4. A visual summary of the results is presented in Figure 3.1, which is discussed at the end of the results.

3.3.1. VARIATION IN FOOD RESOURCE AVAILABILITY - $\mathrm{PCA}_{\mathrm{food}}$

The PCA of the eight food plants (Table 3.1) resulted in five independent principal components, which accounted for 79.65% of the variation in the original data (Table 3.2). The first principal component relates negatively to the two candle cactus species, kadushi (*Subpilocereus repandus*) and datu (*Ritterocereus griseus*). Black willow (*Capparis odoratissima*) and datu are negatively associated with component two. Component three relates positively with cossie (*Acacia tortuosa*) and negatively with West Indian birch (*Bursera simaruba*) and mesquite (*Prosopis juliflora*). Calabash (*Crescentia cujete*) loads strongly and positively on component four. Mesquite also relates positively with component four and yellowwood (*Casearea tremula*) relates negatively. Component five relates positively to cossie and West Indian birch.

3.3.2. VARIATION IN POSSIBLE COMPETITOR ABUNDANCE – $\mathrm{PCA}_{\mathrm{competitors}}$

The PCA of the seven bird species (Table 3.1) resulted in four independent principal components, which accounted for 77.54% of the variation in the original data (Table 3.3). The first component relates negatively to the scaly-naped pigeon (*Patagioenas squamosa*) and the pearly-eyed thrasher (*Margarops fuscatus*). The second component is dominated by the yellow-shouldered Amazon parrot and the largely ground-dwelling white-tipped dove (*Leptorila verreauxi*). Two abundant species, the bare-eyed pigeon (*Columba corensis*) and the brown-throated conure (*Aratinga pertinax xanthogenius*) correlate strongly with component three. The fourth component relates negatively to the introduced troupial (*Icterus icterus*), a fruit-eating oriole. Component four also correlates positively with the pearly-eyed thrasher.

Table 3.2. Factor loadings, total and cumulative proportions of the variance explained for five principal components of the food resource variables. Factor loadings of > 0.4 are shown in bold.

Food plants	Component				
	I	II	III	IV	V
Calabash	-0.11	0.39		**0.68**	-0.16
Cossie		0.29	**0.61**		**0.63**
Mesquite	-0.37	-0.23	**-0.43**	**0.45**	0.25
Black willow	0.19	**-0.62**	0.23		-0.14
Yellow wood	-0.38	0.31	-0.25	**-0.44**	-0.30
West Indian birch	0.26		**-0.56**	-0.22	**0.59**
Kadushi	**-0.60**		0.14	-0.28	
Datu	**-0.49**	**-0.47**			0.23
Proportion of total variance	21.48	19.11	16.48	13.030	9.56
Cumulative variance explained	21.48	40.59	57.06	70.09	79.65

Table 3.3. Factor loadings, total and cumulative proportions of the variance explained for four principal components of the bird community variables. Factor loadings of > 0.4 are shown in bold. Species names in full are: brown-throated conure, scaly-naped pigeon, bare-eyed pigeon, white-tipped dove and pearly-eyed thrasher.

Bird species	Component			
	I	II	III	IV
A. barbadensis		**0.69**	-0.25	
B-t conure	-0.38		**0.59**	-0.27
Troupial	-0.25		-0.17	**-0.77**
S-n pigeon	**-0.68**			
B-e pigeon	0.17		**0.72**	0.19
W-t dove	0.14	**0.69**	0.13	-0.15
P-e thrasher	**-0.53**	0.14	-0.14	**0.52**
Proportion of total variance	22.73	20.68	17.81	16.32
Cumulative variance	22.73	43.41	61.22	77.54

3.3.3. FACTORS AFFECTING CLUTCH SIZE

3.3.3.1. Timing of breeding, proximity to key food resource patches and other pairs

Distance to food resource patch was the only independent variable that had a moderately high selection probability with respect to clutch size (SP = 0.77; Table 3.4). This relationship was negative indicating that pairs nesting closer to food hotspots produced more eggs. Support for the importance of the distance to the second neighbour was low (SP = 0.39) and for the number of nests within 200m even lower (SP = 0.23), indicating that areas of high nest density are not necessarily where pairs produce the most eggs.

3.3.3.2. Food resource at the nest

AIC model comparisons suggest that clutch size is positively related to food supply at the nest. High selection probabilities for the abundance of calabash and mesquite ($PCA4_{food}$ – SP = 0.99; Table 3.4) and for cossie and West Indian birch ($PCA5_{food}$ – SP = 0.85), indicate the importance of these food resources.

3.3.3.3. Competitor abundance and predator presence at the nest

Female parrots laid fewer eggs where the abundance of bare–eyed pigeons and brown-throated conures was high ($PCA3_{competitors}$ – SP = 0.78; Table 3.4).

3.3.3.4. Nest structural characteristics

The analysis suggests that female parrots in nests exposed to the elements lay more eggs (SP = 0.86; Table 3.4). No other nest characteristics were supported in the analysis.

3.3.4. FACTORS AFFECTING BROOD SIZE PRIOR TO FLEDGING

3.3.4.1. Timing of breeding, proximity to key food resource patches and other pairs

Selection probabilities of < 0.51 for all independent variables in this model suggest that productivity did not vary with the timing of breeding, was not higher in areas with multiple breeding pairs, nor was it linked to the proximity of food hotspots (Table 3.4).

3.3.4.2. Food resource at the nest

All variables in this analysis received an SP < 0.53 indicating little or no relationship between brood size and food at the nest (Table 3.4).

Table 3.4. Explanatory variable selection probabilities (SP) and coefficients for each of 12 analyses. Productivity response variables included clutch size, brood size prior to fledging and chick asymptotic weight. Different explanatory variables were grouped into four sets for analysis: timing of breeding and proximity to food resource patch and neighbours, food resource at the nest, competitor abundance and predator presence, and nest structural characteristics.

		Timing of breeding and proximity measures				Food resource at nest					Competitor abundance and predator presence				Nest structural characteristics			
		Initiation date	Distance to food patch	Distance to 2nd neighbour	Nests in 200m	PCA1 Food	PCA2 Food	PCA3 Food	PCA4 Food	PCA5 Food	PCA2 Competitor	PCA3 Competitor	PCA4 Competitor	Predator presence	Nest height	Exposure	Entrance area	Floor area
Clutch size	SP	0.33	**0.77**	0.40	0.23	0.23	0.49	0.38	**0.99**	**0.85**	0.27	**0.78**		0.33	0.24	**0.86**	0.25	0.37
	Coef.	-0.05	**-0.25**	-0.08	0.00	0.03	0.12	0.08	**0.55**	**0.32**	-0.04	**-0.25**		-0.05	0.03	**0.31**	0.02	0.07
Brood size prior to fledging	SP	0.51	0.23	0.22	0.22		0.18	0.53	0.48	0.29	0.19	**0.97**		**0.74**	0.24	0.23	0.57	0.58
	Coef.	-0.09	-0.34	-0.30	-0.09		0.01	0.15	0.14	0.05	0.01	**-0.40**		**-0.36**	-0.01	-0.02	-0.14	0.15
Asymptotic weight	SP	0.31	0.29	0.35			0.16	0.35		**0.73**	**0.84**		**0.69**	0.17		**0.94**	0.27	0.19
	Coef.	-0.03	-0.02	-0.05			-0.03	-0.22		**-0.46**	**0.44**		**-0.33**	-0.04		**-0.47**	-0.04	0.01

3.3.4.3. Competitor abundance and predator presence at the nest

There was strong support (SP = 0.97; Table 3.4) for the negative correlation between brood size prior to fledging and the abundance of bare-eyed pigeons and brown-throated conures ($PCA3_{competitors}$). Predator presence was negatively related to brood size prior to fledgling and the inclusion of this variable was highly probable (SP = 0.74).

3.3.4.4. Nest structural characteristics

Cavity area had the highest selection probability in this analysis (SP = 0.58; Table 3.4), but this indicates only a weak (positive) relationship with brood size prior to fledging. Selection probabilities for other variables in this analysis were lower (SP < 0.57) indicating that nest structural characteristics did not strongly influence this productivity measure.

3.3.5. FACTORS AFFECTING CHICK ASYMPTOTIC WEIGHT

3.3.5.1. Timing of breeding, proximity to key food resource patches and other pairs

All variables in this analysis received an SP < 0.35 indicating little or no relationship between chick asymptotic weight and either timing or proximity measures (Table 3.4).

3.3.5.2. Food resource at the nest

A moderately high selection probability for the negative relationship between chick asymptotic weight and the abundance of cossie and West Indian birch ($PCA5_{food}$ – SP = 0.73; Table 3.4) indicates chicks in areas where these tree are abundant reach lower asymptotic weights than chicks elsewhere. No other independent variables were supported in the analysis.

3.3.5.3. Competitor abundance and predator presence at the nest

The abundance of *A. barbadensis* and white-tipped doves ($PCA2_{competitors}$ – SP = 0.83; Table 3.4), and troupials ($PCA4_{competitors}$ – SP = 0.69) were positively correlated with chick asymptotic weight, whereas pearly-eyed thrashers (also $PCA4_{competitors}$) were negatively correlated with chick asymptotic weight.

3.3.5.4. Nest structural characteristics

Nest exposure was the only independent variable to receive a high selection probability (SP = 0.94; Table 3.4). The relationship was negative indicating that chicks in exposed nests reached lower asymptotic weights.

3.3.6. SUMMARY - EFFECT OF HABITAT VARIABLES ON MEASURES OF PRODUCTIVITY

Figure 3.1 summarizes the results from all 12 analyses. This figure allows visual comparison of how the different habitat variables (left to right) affect productivity measures (top to bottom), and the direction of the relationship (positive or negative).

For clutch size, at least one variable from each set of factors was strongly supported ($SP > 0.7$). The direction of these relationships varied from the positive effect of food resource at the nest to the negative effect of competitor species abundance. By contrast, in the analyses of factors affecting brood size prior to fledging only negative correlations with variables in the competitor abundance and predator presence analysis were strongly supported. Correlations between chick asymptotic weight and variables in three analysis sets received high selection probabilities ($SP > 0.7$). These include both positive and negative relationships with other bird species and a negative correlation with nest exposure.

3.3.6.1. Timing of breeding, proximity to key food resource patches and other pairs

The timing of breeding and proximity to key food resource patches and other pairs appears to be most important to clutch size. Distance to food resource patch in particular had a strong negative influence (SP = 0.77) on clutch size. There is some support for an influence of initiation date on brood size as well (SP = 0.51), but little support for an effect on nestling weight ($SP < 0.35$).

3.3.6.2. Food resource at the nest

Food at the nest appears to most strongly affect clutch size. Calabash and mesquite ($PCA4_{food}$ – SP = 0.99), and cossie and West Indian birch ($PCA5_{food}$ – SP = 0.85) all correlated positively with clutch size. Food resource at the nest did not exert any large influence on brood size prior to fledging ($SP < 0.53$), and there was only moderate support for a negative effect of cossie and West Indian birch on chick asymptotic weight (SP = 0.73).

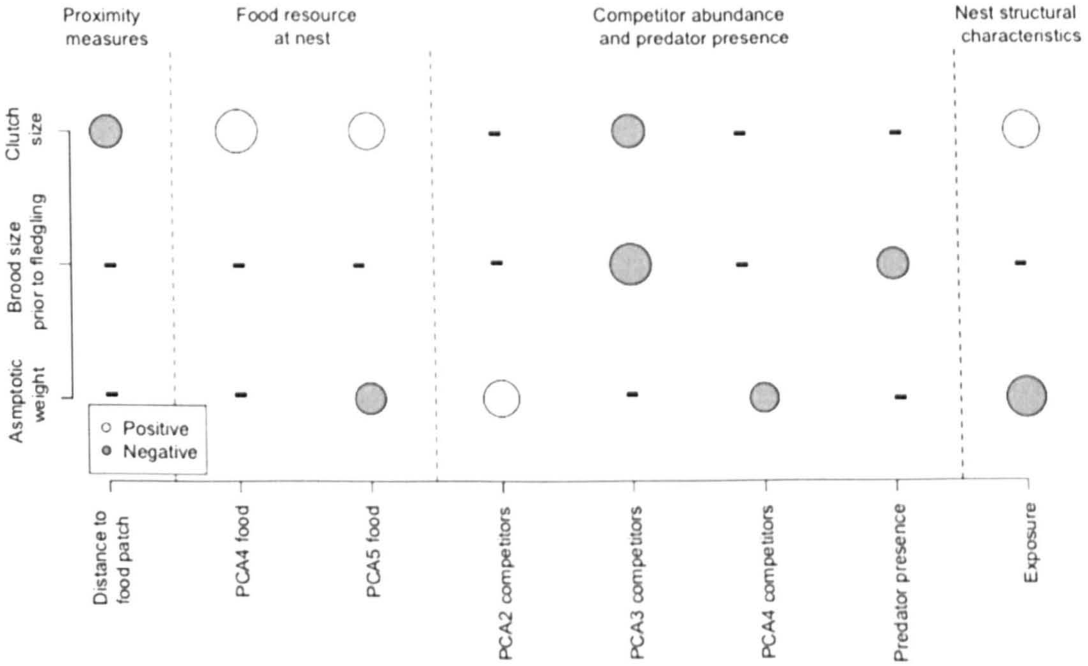

Figure 3.1. Summary of the 12 analyses of factors affecting productivity for *Amazona barbadensis* on Bonaire, Netherlands Antilles, showing only factors with selection probabilities > 0.69. Productivity response variables include clutch size, brood size prior to fledging and chick asymptotic weight. Different explanatory variables were grouped into four sets for analysis: timing of breeding and proximity to food resource patch and neighbours, food resource at the nest, competitor abundance and predator presence, and nest structural characteristics. Circle size represents the independent variable selection probability in the particular analysis. Circle colour represents the direction of the correlation between the dependent and independent variable.

3.3.6.3. Competitor abundance and predator presence at the nest

There were strongly supported competitor and predator variables relating to each productivity measure. The abundance of bare-eyed pigeons and brown-throated conures $PCA3_{competitors}$ was negatively correlated with clutch size (SP = 0.78). In contrast to the above analyses of timing and proximity, and food resource at the nest, competitor and predator variables had moderate to strongly supported negative effects on brood size prior to fledging and chick asymptotic weight. The former again correlated negatively with pigeons and conures ($PCA3_{competitors}$ – SP = 0.97) and also predator presence (SP = 0.74). Chick asymptotic weight was positively correlated with the abundance of *A. barbadensis* and white-tipped doves ($PCA2_{competitors}$ - SP = 0.83), and with troupials $PCA4_{competitors}$, but within the same component was a negative relationship with pearly-eyed thrashers (SP = 0.72).

3.3.6.4. Nest structural characteristics

The only nest structural characteristic to receive strong support in any analysis was exposure. Clutch size was positively related to exposure (SP = 0.86) whereas chick asymptotic weight was negatively correlated (SP = 0.94). Low support was achieved for a negative effect of nest entrance area (SP = 0.57) and a positive effect of cavity area (SP = 0.58) on brood size prior to fledging.

3.4 DISCUSSION

3.4.1. OVERVIEW

In this study I have demonstrated that a range of factors correlate with the productivity of *A. barbadensis* on Bonaire. Pairs in close proximity to food resource patches produced bigger clutches, as did those with greater food resources at the nest. Clutch size was also lower when the abundance of bare-eyed pigeon and brown-throated conures was higher. These two species also correlated negatively with brood size prior to fledging. Conspecifics and other bird species correlated positively with asymptotic weight. Predator presence correlated negatively with brood size prior to fledging and nest characteristics were found to correlate positively with clutch size but negatively with chick asymptotic weight.

3.4.2. TIMING OF BREEDING

The timing of breeding is important in seasonal environments with productivity typically declining as the season progresses (Norris, 1993). However, I detected no relationship between nest initiation date and productivity for *A. barbadensis* on Bonaire.

3.4.3. PROXIMITY TO OTHER PAIRS

Parrots appear to show a preference for nesting in clusters (Snyder et al., 1987; Smith, 1991; Enkerlin-Hoeflich, 1995; Garnett et al., 1999). On Bonaire, the distribution of *A. barbadensis* nests is clustered (discussed further in the following chapters). However, neither measure of clustering used in the analyses (distance to second neighbour or nests within 200 metres) was strongly supported as a predictor of productivity, indicating that nests in high-density areas are not more productive than those in other areas.

There are a number of reasons why no pattern between neighbour proximity and productivity were found. First, perhaps the density measurement is inappropriate and there may be no such clustering if nest density was measured relative to resource distribution, i.e. the number of nests per unit of food resource. If productivity did not vary with nest density per resource, the observed nest clusters could be described as an ideal free distribution (Fretwell & Lucas, 1969). Second, perhaps the productivity measurement is inappropriate: the benefit of clustered nesting may only be evident during the first weeks immediately post fledging when chick mobility is low, and survival may also be low. For example, increased predator detection during the vulnerable post-fledging period would not have been detected in this study. Alternatively, it may be that clustered nesting is not a preference but rather the result of nest site limitation. The fitness benefit or limitation that drives the observed clustered nesting in many parrots has not been successfully identified by any study to date and this topic clearly deserves further study.

3.4.4. PROXIMITY TO FOOD RESOURCE PATCHES AND FOOD RESOURCE AT THE NEST

The importance of food as a limiting factor for survival and productivity is well known, but the mechanism by which it affects individuals can be complex (Cody, 1974; Kenward & Sibly, 1977; Holmes et al., 1979; Martin, 1987; Newton, 1998). The proximity of food resource patches and two food components correlated positively with clutch size indicating that females with greater access to food laid more eggs. Access to this resource may be important in allowing females to reach breeding condition (Ankney & MacInnes, 1978; Newton et al., 1983).

Access to a high quality food resource whether in a patch or around the nest may also be important prior to breeding because of competition for nest sites. This competition can be fierce and even during the non-breeding season pairs may be found around their nest (pers. obs.). Intense competition for cavities is typical in cavity-nesting species. For example, in northern Australia, female eclectus parrots (*Eclectus roratus*) spend up to 9 months guarding cavities and take-over attempts may result in the death of a female (Heinsohn & Legge, 2003). Starlings (*Sturnus vulgaris*) are also particularly dominant nest competitors that frequently take over cavities used by other species. In Europe they out-compete nuthatches (*Sitta europaea*) and in North America where starlings are introduced they outcompete eastern bluebirds (*Sialia sialis*) (Pinkowski, 1976; Nilsson, 1984). During my research, three cases of chick infanticide were confirmed, indicating that competing pairs do investigate active nests when there is an opportunity, and may attempt take-overs. In 19 clutches (23% of 84), the first egg was damaged before the second egg was laid and although no cases were confirmed, it was suspected that this damage was caused by competing pairs in several cases. Thus, having to forage at distant or low quality food sources would require time away from the nest, which could present opportunities for prospecting pairs to investigate and disrupt breeding attempts.

Most of the important food resource patches identified in this study were small fruit plantations or collections of gardens, and the fruit trees in these areas are largely exotic species such as almond (*Terminalia catappa*), canepa (*Melicoccus bijugatus*) and mango (*Mangifera indicia*). The apparent importance of these patches suggests that natural habitats can be enhanced for breeding parrots with introduced plant species. However, a critical feature of the food resource patches that may ultimately drive their importance to parrots is water, whether it is a ground water source, a spring or irrigation. On this dry island, as in other dry tropical forest areas, water is a fundamental requirement for fruiting trees (Renton, 2001). In the absence of exotic fruit trees, native plants species in these areas that experienced the same conditions would probably be relatively productive as well.

Food limitation in species with asynchronous broods often results in the smallest chick dying of starvation (Lack, 1968; Stenning, 1996; Stoleson & Beissinger, 1997; Smiseth et al., 2003). Such mortality has been observed in Amazon parrots (Fernandes Seixas & Mourão, 2002; Renton & Salinas-Melgoza, 2004), but over the course of this study very few parrot chicks (<5%) died in situations where starvation was confirmed as the cause of mortality. This might explain the lack of support for the effect of food resource variables on brood size prior to fledging during the three years of observations. In drier years when fruit production would be lower, it is likely that food limitation becomes more important.

3.4.5. COMPETITOR ABUNDANCE AT THE NEST

A. barbadensis pairs have smaller clutches and rear fewer chicks to fledging age where the abundance of bare-eyed pigeons and brown-throated conures is high. This negative relationship may be causal, but without experimental evidence this cannot be determined. The pattern of lower *A. barbadensis* productivity in areas of high pigeon and conure abundance could arise from differences in habitat preferences. High quality habitat for *A. barbadensis* with good productivity may not be high quality habitat for pigeons and conures, so they are less abundant in those areas. Alternatively, high quality *A. barbadensis* pairs that are productive may be more aggressive and exclude possible competitors from the food resource in the vicinity of their nest. Further study is needed to determine whether the observed correlation is the result of pigeons and conures having a negative effect on *A. barbadensis*, a result of habitat preferences or a result of competitive behaviour.

Chick weight was positively correlated with the abundance of other *A. barbadensis* and the ground-dwelling white-tipped doves. This pattern is presumably a simple association whereby other parrots, and doves, show a preference for food-rich areas where breeding pairs are productive.

3.4.6. PREDATOR PRESENCE AT THE NEST

It is no surprise that introduced rats had a negative effect on the number of offspring reaching fledgling age. The negative impact of introduced mammalian predators on oceanic island bird populations is well known (Robinet et al., 1998; Jones, 2005; Igual et al., 2007; BirdLife, 2008a). Any potential benefits of clustered nesting for increased predator detection received little support because there was no evidence of increased brood size in areas of higher nest density.

3.4.7. NEST CHARACTERISTICS

Nest site characteristics have been shown to influence various measures of fitness in many bird species (Dawson et al., 2005; Ost et al., 2008; Ardia et al., 2009). The dimensions of nest cavities used by *A. barbadensis* on Bonaire range widely (Chapter V), and the only variable that correlated with a productivity measure, and received strong support, was nest exposure.

Life history theory assumes trade-offs in the use of limited resources, so females should trade-off current and future reproductive investment (Charnov & Krebs 1974). Thus, a female using an exposed nest might be expected to reduce costs by laying a smaller, less energy demanding, clutch, assuming there may be an opportunity to nest in a less exposed cavity for future breeding attempts. In light of the above, the observation that *A. barbadensis* females produce larger clutches in more exposed nests is curious. It may be that there are more complex variations in investment that confound this analysis. For example, variable female reproductive investment may be reflected in egg size or contents (Williams & Cooch, 1996; Russell et al., 2007). Furthermore, differences in investment may result from factors other than nest exposure, such as predation risk, female body condition and partner quality (Eggers et al., 2006; Ardia et al., 2009).

As with incubating females the nestlings of altricial birds must trade off the investment of their limited resources, for either growing or thermoregulation (Ricklefs et al., 1994). *A. barbadensis* chicks in less exposed nests reached a higher asymptotic weight, independent of brood size, as would be expected (Ricklefs et al., 1994; Dawson et al., 2005). In many species, heavier offspring achieve greater fitness (Lindstrom, 1999), and since *A. barbadensis* is a long-lived species, offspring quality may have profound fitness consequences. However, examining the full extent of these possible fitness gains would be a formidable undertaking in a species that may live over 30 years.

3.4.8. CONCLUSION

This study shows that a range of factors influence various components of productivity in the Bonaire population of the yellow-shouldered Amazon parrot. Nest density was not correlated with any productivity measure, however there were a number of unanswered questions relating to clustered nesting and this topic is certainly worthy of further study. Access to food resources on two spatial scales correlated positively with female investment (clutch size), however the mechanism by which food limitation influences breeding parrots was not determined and may be a combination of direct and indirect processes. Productivity correlated negatively with other bird species but further study is necessary to determine whether this is a causal relationship. Introduced mammalian predators had a negative effect on brood size. Predator control is now an established component of conservation and this should be considered for future conservation management. Nest cavity characteristics, specifically exposure, was associated with larger clutches, which is a curious result needing further investigation, but also with reduced chick asymptotic weight, probably as a result of increased thermoregulatory costs.

These findings identify key links between features of the yellow-shouldered Amazon parrot's biology and its habitat. They provide some of the highest resolution data on these relationships for large parrots, and should be valuable to conservation managers. However, while the management of many of the habitat and life history features may be conveniently realistic (e.g. increasing food to boost investment in the current reproductive effort, controlling predators to reduce offspring mortality, enhancing nest sites to reduce their exposure), this study does not detail patterns of post-fledging and adult survival. It is important to recognise that from a conservation standpoint these are likely to be critical aspects of parrot demography.

Chapter IV

SPATIAL AND TEMPORAL DISTRIBUTION OF AMAZONA BARBADENSIS ON BONAIRE

4.1. INTRODUCTION

Understanding the factors that affect species' distributions is central to the study of ecology and is essential for long-term conservation initiatives. Theory predicts that individuals will distribute themselves in order to maximise their fitness (Fretwell & Lucas, 1969; Parker & Sutherland, 1986; Morris, 2003). Numerous classic studies have demonstrated how individuals preferentially select spatially and temporally higher quality habitat (Andrewartha, 1954; MacArthur, 1958; Holmes et al., 1979; Milinski, 1984). One of the most important steps in developing an understanding of species' distributions is to assess the key factors driving the observed patterns of abundance (Varley et al., 1973). Population growth is regulated, and over heterogeneous landscapes where there may be profound differences between habitat types, source-sink population dynamics may exist (Pulliam, 1988; Sinclair, 1990; Sibly et al., 2007).

Being able to determine and predict species' distributions is an important goal for ecologists and this area of study has a long history (Andrewartha, 1954; MacArthur & Wilson, 1967). More recently there has been considerable focus on understanding how species respond to human impacts on global ecosystems, specifically global climate change (Schweiger et al., 2008; Thuiller et al., 2008). On smaller scales, identifying areas of high habitat quality is important for conservation managers who are seldom able to protect the entire range of a species and must therefore prioritise key areas (BirdLife, 2009; CEPF, 2009; Plantlife, 2009).

The biotic and abiotic factors that make a habitat unsuitable for a species may include intense predation pressure, high competition, low resource availability, or environmental factors (Connell, 1961; Cameron, 2006; Eggers et al., 2006; Chalfoun & Martin, 2007; Ritchie et al., 2009). Connell's (1961) classic work examined the vertical distribution of two barnacle species. Desiccation, an abiotic factor, limited the upper range of the competitively superior *Balanus balanoides* whereas the lower range of *Chthamalus stellatus* was limited by the presence of *Balanus*. When *Balanus* was experimentally removed the competitively inferior *Chthamalus* was able to occupy lower strata of rocks. More recently, species distribution modelling has been used to indentify complex combinations of inter-specific competition and abiotic environmental factors. Using an information theoretic approach and comparing competing model Akaike weights Ritchie et al. (2009) found that the ecologically similar antilopine wallaroo (*Macropus antilopinus*) and eastern grey kangaroo (*Macropus giganteus*) compete. This influenced their distribution as did different environmental factors. By contrast there was no competitive relationship with the ecological dissimilar common wallaroo (*Macropus robustus*), the distribution of which is influenced mostly by climate. Although at a very different scale to Connell's (1961) work, this study was able to disentangle the effects of competition and environmental conditions for three wide ranging species and show that competition between two ecologically similar species contributed to smaller realised niches for each species than their fundamental niche.

The seasonal migrations of birds are one of the most obvious responses of all animals to variations in environmental conditions in temperate areas (Reid et al., 2003; Van der Jeugd et al., 2009), and abiotic factors such as rainfall may also have a pronounced effect on species' distributions in tropical systems (Renton, 2001). At a given location, habitat structure may also influence the distribution of birds through a variety of mechanisms including its effect on predation risk, competition or resource availability (Cowie & Simons, 1991; Yue-Hua & Yu, 1994; Illera, 2001; Whittingham et al., 2005; Bellis et al., 2006; Castillo & Eberhard, 2006; Chalfoun & Martin, 2007; Hinam & Clair, 2008). Even the same limiting factor can manifest in different ways in the same habitat. For example, in an early study using a trained goshawk (*Accipiter gentilis*), Kenward (1978) showed that wood pigeon (*Columba palumbu*) mortality was higher in complex habitats where predator detection was harder. By contrast, in hazel grouse (*Bonasa bvnasia*) and dickcissels (*Spiza americana*), predation rates were lower in more structurally complex woodland areas (Yue-Hua & Yu, 1994; Berkeley et al., 2007).

Parrots are a worthy but challenging group in which to investigate spatial and temporal distribution. They are one of the most at risk groups of organisms on the planet, inhabiting some of the world's most threatened wilderness areas (Bennett & Owens, 1997; Snyder et al., 2000; Juniper & Parr, 2003; Ricketts et al., 2005). Many species inhabit seasonal environments with ephemeral food resources, and consequently, they track resource availability through nomadic or even migratory movements (Smith & Rowley, 1995; Drechsler, 1998; Renton, 2001; Karubian et al., 2005; Salinas-Melgoza & Renton, 2005; Manning et al., 2007), while having to be responsive to predation risk (Snyder et al., 1994; Smith & Rowley, 1995; Beissinger et al., 2008) and resource competition (Snyder et al., 1987; Heinsohn et al., 2003). Critically, several conservation initiatives include the release of individuals to reintroduce or augment wild populations (Sanz & Grajal, 1998; Snyder et al., 2000; Collazo et al., 2003), yet there are very few detailed studies of parrot distribution and habitat requirements. This is almost certainly due to the challenging environments in which many parrots are found, such as remote tropical rainforests.

In this study I investigate a range of factors that theory and previous research suggest will be important to the spatial and temporal distribution of the yellow-shouldered Amazon parrot (*Amazona barbadensis*), a vulnerable species (IUCN, 2008) on the oceanic island of Bonaire, Netherlands Antilles. Specifically, I examine the effect of small-scale variation in habitat structure and bird community on spatial distribution, and the effect of the previous month's rainfall on the island wide temporal distribution.

Examining the factors affecting the spatial and temporal distribution of *A. barbadensis* is justified for the following three reasons: First, parrots occur throughout tropical forested areas and appear to prefer taller more mature vegetation structure (Rowley & Chapman, 1991; Marsden et al., 2000). For many parrot species this is nearly impossible to study, however, the low vegetation on Bonaire makes this an outstanding study system relevant to other parrots. Breeding birds in particular are dependent on mature trees in which nest cavities may be found (Juniper & Parr, 2003). Second, there has been almost no study of shared resource or habitat use, or competition between endangered island parrot species and other birds in the community. This is particularly relevant for conservation, following the widespread introduction of alien bird species (MacArthur & Wilson, 1967). Finally, in dry environments rainfall has a profound effect on plant phenology, which in turn can influence parrot feeding behaviour and distribution (Renton, 2001; Salinas-Melgoza & Renton, 2005; Sanz & Rodríguez-Ferraro, 2006).

4.2. METHODS

4.2.1. STUDY AREA AND SPECIES

This study was conducted on Bonaire, an oceanic island (288km^2) of the Netherlands Antilles. Bonaire is in the Southern Caribbean Sea between 68° 11' - 68° 25' West and 12° 1' - 12° 9' North (Figure 4.1). The island has an average annual temperature of 28°C and receives low, irregular and localised rainfall. The average annual precipitation is 463mm, of which 51% falls in October, November and December. The xerophytic vegetation is highly heterogeneous and has been degraded dramatically since European colonisation and the introduction of free-ranging goats (De Freitas, 2005).

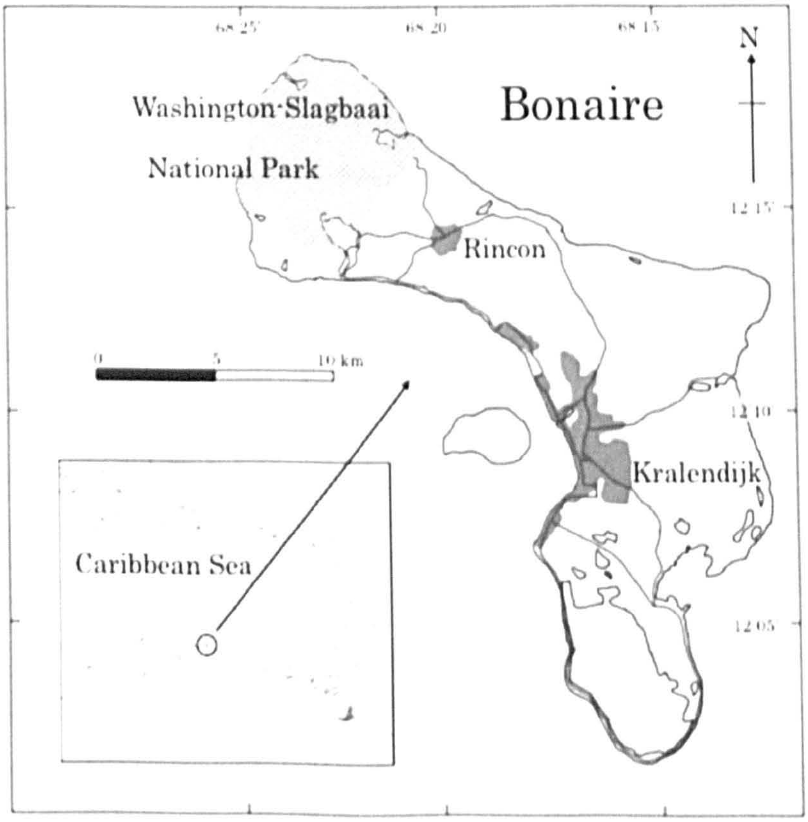

FIGURE 4.1. Location of Bonaire, Netherlands Antilles, Caribbean. *Amazona barbadensis* is distributed throughout the northern three quarters of the island.

A. barbadensis is a medium-sized parrot (275-365g). Its distribution on Bonaire is widespread but excludes the southern quarter of the island, south of Kralendijk (Figure 4.1), which is largely a windswept wetland area. Like most parrots *A. barbadensis* roosts in raucous groups that on Bonaire can include several hundred individuals.

Particular roosts were used faithfully throughout the study, although the distribution of individuals among roosts varied temporally. Breeding typically takes place between May and August, and nests are found in clusters or in isolation across the island, north of Kralendijk. During the breeding season *A. barbadensis* pairs exclude other pairs from the immediate vicinity of their nest.

4.2.2. HABITAT STRUCTURE

At 15 nest sites, seven key foraging areas and 27 random locations I measured eight habitat variables, described in Table 4.1. These measurements provided a coarse assessment of the vegetation height, structure and composition as well as the extent of vegetation coverage. Random locations were selected by generating a series of six figure grid references used in combination with a topographical map. At each location I marked out a $10m^2$ quadrat and recorded the eight habitat variables.

4.2.3. SPATIAL ABUNDANCE OF PARROTS AND OTHER BIRDS

The abundance of *A. barbadensis* and six possible competitor bird species was counted at each of the quadrats. I made a minimum of three and a maximum of six visits to each site to conduct 15-minute morning (0600-0900hrs) or evening (1500-1900hrs) bird counts between May and August. Any bird heard or seen within 50 meters of the quadrat was recorded. Mean values of these counts were calculated for each site. These variables are described in Table 4.1.

4.2.4. CONTROL VARIABLES

Access to suitable habitat may depend on proximity to roost locations. To control for this, I measured the distance to the nearest roost from each quadrat using a hand held GPS unit. Quadrats were grouped by site type: nest, foraging or random site, to account for possible bias from their inclusion.

4.2.5. TEMPORAL PARROT DISTRIBUTION AND RAINFALL

I visited eight *A. barbadensis* roost sites monthly or opportunistically when on Bonaire, to count the number of individuals. Four of these roost sites were in urban areas and four were in rural areas. Counts were made at the different sites on consecutive mornings and evenings. Other smaller roosts, also used by *A. barbadensis*, were not observed and therefore the counts were not a complete population census. Rainfall data were obtained from the Bonaire Organisation of Petroleum Exporting Companies

(BOPEC), which is located in the north of Bonaire. Monthly rainfall totals were used in the analysis of the temporal distribution of *A. barbadensis*.

Table 4.1. Potential explanatory variables for the spatial distribution of *Amazona barbadensis* on Bonaire, Netherlands Antilles.

Explanatory variable	Description	Justification
Maximum height of vegetation	Measured in cm	Parrots prefer taller habitat (Marsden et al 2000)
Number of tall trees	Count of trees > 4m in height	
Number of big trees	Count of trees with circumference at breast height > 30cm	Many mature trees on Bonaire have a large girth but are not tall
Tree species richness	Count of trees > chest height	Potential indicator of habitat regeneration
Total woody plants	Count of all woody plants	Alternative potential indicator of habitat regeneration
% Coverage open	Estimate from an assumed aerial view	Estimate of unsuitable area
% Coverage all trees	Estimate from an assumed aerial view	Estimate of the "canopy" closure
% Coverage Cacti	Estimate from an assumed aerial view	Estimate of specific food/water resource
Brown-throated conure (*Aratinga pertinax xanthogenius*)	15minute bird count at dawn (0600 - 0900) or dusk (1600 - 1900) within a 1ha quadrat centered on the nest (Northern edge 50m north of the nest)	Abundant endemic subspecies, only other parrot, observed diet overlap
Troupial (*Icterus icterus*)		Abundant and introduced, observed diet overlap
Scaly-naped pigeon (*Patagioenas squamosa*)		Large fruit eaters, observed diet overlap
Bare-eyed pigeon (*Columba corensis*)		
White-tipped dove (*Leptorila verreauxi*)		Observed diet overlap
Pearly-eyed thrasher (*Margarops fuscatus*)		Known nest competitor, causing offspring mortality, (Snyder et. al. 1987)
Distance to nearest roost	Measured in metres by GPS	Access to suitable habitat may depend on proximity to roost locations
Quadrat type	Nest, feeding or random site	Control

4.2.6. QUESTIONS

My overall objectives were to explore how the distribution of *A. barbadensis* varied spatially in relation to habitat structure, bird community and distance from roost sites;

and to investigate how the distribution of *A. barbadensis* across the islands varies temporally in relation to rainfall. Specifically, I examined:

1. Whether the spatial abundance of *A. barbadensis* correlates with habitat structure?
2. Whether the spatial abundance of *A. barbadensis* correlates with other bird species in the community?
3. The relative importance of habitat structure measures and bird species abundances on the spatial abundance of *A. barbadensis*?
4. Whether *A. barbadensis* move between urban and rural sites?
5. The effect of rainfall on the distribution of *A. barbadensis* between urban and rural areas.

4.2.7. STATISTICS

All statistical analyses were conducted in the R environment (R Development Core Team, 2009). My response variable in analyses of spatial distribution was the abundance of *A. barbadensis* as measured at each nest, feeding or random quadrat site. I examined the spatial abundance of *A. barbadensis* as a function of habitat, bird species, proximity to nearest roost and quadrat type. For the temporal distribution analysis my response variable was the total count of *A. barbadensis* at the four urban and the four rural roosts. I examined the temporal abundance of *A. barbadensis* as a function of the total rainfall in the previous month.

To reduce the number of habitat and bird species explanatory variables in the spatial distribution analysis, I conducted a principal component analysis (PCA) on the habitat variables and a second PCA on the bird community counts. The spatial abundance of *A. barbadensis* was then modelled against the habitat principal components, controlling for the distance from the roost and quadrat type. A second analysis examined the abundance of *A. barbadensis* against the bird community principal components controlling for distance to the roost and group. All spatial distribution data were initially examined for spatial autocorrelation using a generalized least squares function specifying the distribution of all quadrats using latitude and longitude (Pinheiro & Bates, 2000). I found no evidence of spatial autocorrelation in these data.

In each analysis, I used a general linear model (GLM) with a Poisson error distribution structure. I used an information theoretic approach (Burnham & Anderson, 2002) to select appropriate explanatory models. This approach compares all possible candidate models under a maximum model using Akaike's Information Criterion. The Akaike values (AIC) of different models can be directly compared by their difference (Δ_i) to the best fitting model, which has the smallest AIC. Model residuals from the AICc best model were visually assessed for normality. In each analysis (habitat and birds) all possible variations of the model were fitted. These permutations were then ranked from best to worse on their AICc. Akaike weights (w_i) were also calculated for each model. The w_i is the probability that model *i* would be included in the final model.

The 95% confidence set of models is the smallest subset of candidate models for which the Δ_i sum to 0.95. Within the confidence set of each analysis the Akaike weights were recalculated to sum to 1, as recommended by Burnham and Anderson (2002).

Akaike weights were also calculated for each explanatory variable (*k*) from the confidence set. This estimates the probability that of all the variables considered, k^{th} *variable* would be in the best model. The explanatory variable selection probabilities and coefficients (β) for each explanatory variable were also recalculated from the confidence set. As the ratio of observations (n) to *k* was low (both analyses) the second-order criterion AICc was used to produce likelihood-based measures of model fit.

The information theoretic approach works best with as few explanatory variables as possible (Whittingham et al., 2006). Specifically the number of possible model permutations (directly related to *k*) should not exceed the number of observations (Burnham & Anderson, 2002). Various constraints limited the data available for each analysis. To compare the relative impact of the habitat and bird community variables on the spatial abundance of *A. barbadensis*, I conducted a third analysis, which combined the variables with high selection probabilities from the earlier habitat and bird community analyses. This approach was necessary in order to achieve an acceptable ratio of n/*k*. Distance to roost and quadrat type were also included in the third analysis.

Temporal patterns of distribution were examined first by the correlation between urban and rural roost densities over the course of three years. A negative correlation would suggest an annual cycle of "migration" from urban, dry season roosting sites (approximately March to August), to rural, rainy season roosting sites (approximately September to February). I also used a GLM to test whether this seasonal pattern was driven by the effect of the previous month's rainfall, using the total number of *A. barbadensis* in four urban roosts and in four rural roosts.

4.3. RESULTS

4.3.1. VARIATION IN HABITAT STRUCTURE

The PCA of the eight habitat structure variables (Table 4.1) resulted in five independent principal components, which accounted for 80% of the variation in the original data (Table 4.2). The first principal component can be summarised as habitat maturity as it relates (inversely) to the percentage cover of all trees, trees over four meters in height (Tall trees) and trees greater than 30cm in girth (Big trees). Principal component two relates to bare ground, with the percentage of open cover increasing as the percentage cover of cacti and the number of woody plants both decrease. The number of trees (richness) and the percentage cover of cacti both relate positively to component three, trees and cacti. As the number of trees and cacti increase in this component the total number of woody plants, including smaller shrubs, decreases. Component four relates negatively to the number of tall trees (>4m), and the number of trees. Again tree richness contrasts with the number of woody plants, which increases, as does the percentage cover of cacti as the two tree counts decrease.

Table 4.2. Factor loadings, total and cumulative proportions of the variance explained by habitat structure principal components. Factor loadings of > 0.4 are shown in bold.

Habitat structure variables	Component			
	I	II	III	IV
Big trees	**-0.43**	0.22	0.15	0.26
Tall trees	**-0.44**	0.13	0.15	**-0.65**
Tree richness	-0.34	-0.33	**0.69**	**-0.41**
Woody plants	-0.21	**-0.41**	**-0.64**	**0.56**
Max height	-0.39	0.18	0.33	-0.25
% Open	0.28	**0.66**	0.16	0.26
% Trees	**-0.46**	-0.12	0.11	-0.36
% Cacti	0.14	**-0.53**	**0.57**	**0.48**
Proportion of total variance	0.41	0.17	0.14	0.09
Cumulative variance explained	0.41	0.57	0.71	0.80

4.3.2. VARIATION IN BIRD ABUNDANCE

The PCA of the six potential competitor bird species (Table 4.1), resulted in four independent principal components, which accounted for 84% of the variation in the original data (Table 4.3). Component one relates negatively to the scaly-naped pigeon (*Patagioenas squamosa*), pearly-eyed thrasher (*Margarops fuscatus*) and the white-tipped dove (*Leptorila verreauxi*). The bare-eyed pigeon (*Columba corensis*) loads very strongly and negatively on principal component two. Also strongly loaded on component two are the introduced troupial (*Icterus icterus*) and the brown-throated conure (*Aratinga pertinax xanthogenius*), which both increase as the abundance of bare-eyed pigeons decreases. The only strongly loading variable on component three was the white-tipped dove, which correlated negatively. Component four relates to three species: the troupial and white-tipped dove, which decrease as the pearly-eyed thrasher increases.

Table 4.3. Factor loadings, total and cumulative proportions of the variance explained by bird community principal components. Factor loadings of > 0.4 are shown in bold. Species names in full are: brown-throated conure, scaley napped pigeon, bare-eyed pigeon, white-tipped dove and pearly eyed thraher.

Bird community variables	Component			
	I	II	III	IV
B-t conure	-0.36	**0.59**	-0.17	-0.23
Troupial	-0.25	**0.65**	0.39	**-0.52**
S-n pigeon	**-0.52**	-0.29	-0.34	0.26
B-e pigeon	0.18	**-0.91**	-0.27	0.26
W-t dove	**-0.49**	-0.13	**-0.74**	**-0.41**
P-e thrasher	**-0.52**	-0.34	0.19	**0.41**
Proportion of total variance	0.30	0.23	0.18	0.14
Cumulative variance explained	0.30	0.53	0.70	0.84

4.3.3. FACTORS AFFECTING SPATIAL DISTRIBUTION

4.3.3.1. Habitat structure principal components

The AIC best model explaining the spatial distribution of *A. barbadensis* abundance across Bonaire included the explanatory variable relating to habitat maturity

($PCA1_{habitat}$) and the quadrat type control. The abundance of *A. barbadensis* was positively correlated with habitat maturity, i.e. areas with increasing amounts of tree cover, tall trees (>4m) and big trees (girth >30cm). Of the other principal components, $PCA3_{habitat}$, which relates to trees and cacti, had the second highest selection probability, however, this was very low (0.33). It is important to note that in AIC analyses variables with poor explanatory power are not expected to have a selection probability of zero. Distance to the nearest roost was not strongly supported (0.32), indicating that *A. barbadensis* distribution is not restricted to areas near roost locations. Quadrat type had a high probability of selection (0.99). *A. barbadensis* was most abundant in food area quadrats, moderately abundant in nesting areas and least abundant in random areas.

4.3.3.2. Bird abundance principal components

Of the bird abundance principal components only component one, relating negatively to scaly-naped pigeon, thrasher and dove, was included in the AIC best model along with quadrat type. The abundance of *A. barbadensis* was greater in areas where the abundance of these possible competitors was greater. Other bird abundance principal components did not receive strong support. Similarly support for distance to the nearest roost was again low (0.22). Quadrat type received strong support (0.83). The pattern of *A. barbadensis* abundance by quadrat type was the same as the habitat analysis with increasing abundance from random areas to nest areas, with the greatest abundance in feeding areas.

4.3.3.3. Habitat structure and bird abundance principal components combined

The two most highly supported principal components from each of the habitat structure and bird abundance analyses were included in this analysis along with quadrat type and the distance to the nearest roost (Table 4.4). Overall, the two bird abundance components received slightly more support than the two habitat components. Of the explanatory variables the abundance of scaly-naped pigeons, thrashers and doves ($PCA1_{birds}$) had the highest selection probability (0.98). *A. barbadensis* abundance increased with increasing abundance of these possible competitor species. Habitat maturity had the second highest selection probability (0.75) with greater *A. barbadensis* abundance in areas of more mature habitat. The white-tipped dove dominated component ($PCA3_{birds}$) received more support in this combined analysis than in the independent bird abundance analysis but overall this was still only a low level (0.45).

Table 4.4. Models and parameters of the AICc 95% confidence set, from the analysis of factors affecting the spatial distribution of *Amazona barbadensis* on Bonaire, Netherlands Antilles. Explanatory variables include habitat and competitor principal components, distance to the nearest roost and quadrat type, (n = 32). The table indicates the parameters included in the model (I), the number of parameters (*K*), the AICc, delta weight (Δ_i ; difference between the AICc of the given model and the AICc best) and the model selection probability (w_i). The latter we recalculated to sum to one within the confidence set. Parameter estimates (ß) were calculated by summing across the models within the confidence set (weighted by the confidence set model selection probability).

	PCA1-habitat	PCA3-habitat	PCA1-competitors	PCA3-competitors	Distance to roost	Quadrat type	*K*	AICc	Δ_i	w_i
AICc best	I		I	I			3	213.636	0.000	0.104
	I		I			I	3	213.722	0.086	0.100
	I		I	I	I		4	213.838	0.202	0.094
	I		I		I		3	214.074	0.438	0.084
			I			I	2	214.358	0.722	0.073
	I		I				2	214.587	0.951	0.065
	I		I	I		I	4	214.894	1.258	0.056
		I	I			I	3	214.944	1.308	0.054
	I	I	I			I	4	215.124	1.488	0.050
	I	I	I	I			4	215.555	1.919	0.040
	I		I		I	I	4	215.564	1.928	0.040
	I	I	I	I		I	5	216.074	2.438	0.031
			I	I		I	3	216.139	2.503	0.030
	I	I	I	I	I		5	216.221	2.585	0.029
		I	I	I		I	4	216.443	2.807	0.026
	I	I	I		I		4	216.589	2.953	0.024
	I	I	I				3	216.810	3.174	0.021
	I		I	I	I	I	5	216.876	3.240	0.021
			I		I	I	3	216.912	3.276	0.020
	I	I	I		I	I	5	217.460	3.824	0.015
		I	I		I	I	4	217.564	3.928	0.015
Full model	I	I	I	I	I	I	6	218.600	4.964	0.009
Selection probability	0.78	0.31	1.00	0.44	0.35	0.54				
ß	-0.31	-0.08	-0.87	-0.16	0.13					

In the third analysis the AIC best model for explaining the spatial distribution of *A. barbadensis* abundance across Bonaire included habitat maturity ($PCA1_{habitat}$), scaly-naped pigeons, thrashers and doves ($PCA1_{birds}$), and white-tipped doves ($PCA3_{birds}$). Distance to the nearest roost was not well supported (0.36) and support for quadrat type decreased noticeably in this analysis to 0.53. The pattern of abundance in different sites remained the same with greatest abundance of *A. barbadensis* being observed in food sites and the least in random areas.

4.3.4. VISUALISING THE DISTRIBUTION OF PARROTS AND EXPLANATORY VARIABLES

I mapped the spatial distribution of *A. barbadensis* abundance, habitat maturity ($PCA1_{habitat}$) and bird abundance ($PCA1_{birds}$) using the akima library in R, which interpolates the data to create smooth lines in the form of contour plots (Figure 4.2). *A. barbadensis* is absent from large areas of Bonaire as shown in dark green (Figure 4.2.a). Areas of high abundance are localised and include the two towns, Kralendijk and Rincon (see Figure 4.1), and other key areas such as nesting and feeding sites. The distribution of habitat maturity is shown in Figure 4.2.b. Southern and eastern areas have less mature habitat, that is lower percentage tree cover and fewer tall and big trees, and are represented green. Generally northern and western areas have mostly moderately mature habitat with a few areas of higher maturity habitat. The distribution of possible competitors ($PCA1_{birds}$) is shown in Figure 4.2.c. These bird species overlap considerably with the distribution of *A. barbadensis*. However, the abundance of possible competitor species is more uniform across the island than that of *A. barbadensis*. Although competitor abundance increases around mature habitat areas it does so to a lesser extent than that of *A. barbadensis*. Overall competitor species are not as strongly limited by the maturity of habitat and can occur in higher densities in moderately mature to immature habitat areas.

4.3.5. RAINFALL AND TEMPORAL DISTRIBUTION

There was a significant negative correlation between the number of *A. barbadensis* using urban and rural roosts ($t=-2.344$, $P> 0.05$), i.e. as the number of birds at urban roosts increased, the number at rural roosts decreased (Figure 4.3). Furthermore the number of *A. barbadensis* using urban roosts was negatively correlated with the previous month's rain ($t=-2.364$, $df=12$, $P<0.05$). Whereas the number of

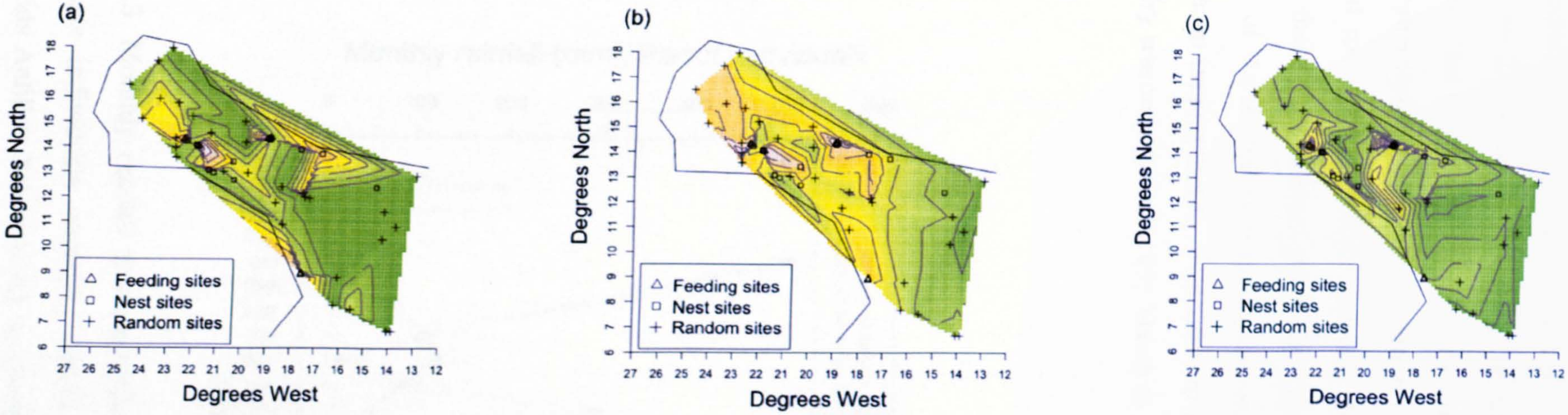

Figure 4.2. Contour plots of (a) *A. barbadensis* abundance, (b) habitat maturity ($PC1_{habitat}$) and (c) possible competitor abundance ($PC1_{birds}$), at nest, feeding, and random sites. Colours indicate terrain as in a topographical map. In a: Green areas represent lower abundance of *A. barbadensis*. Brown and white areas are peaks and represent greater *A. barbadensis* abundance. In b: Brown areas have a higher percentage tree cover and more tall and big trees. Green areas represent immature; areas of lower percentage tree cover and fewer tall and big trees. In c: Green areas have lower abundances of scaly-naped pigeons, thrashers and doves. Yellow and brown areas are peaks and represent greater abundance of these bird species.

A. barbadensis using rural roosts was positively correlated with the previous month's rainfall (t=- 2.128, *df*=12, *P*=0.05). The temporal pattern of these variations in urban and rural roost counts and the monthly rainfall totals can be seen in Figure 4.3. The spatial pattern of this temporal migration is shown in contour plots for all eight urban and rural roosts from January and July 2007 and 2008 (Figure 4.4). The similarity between these plots between years highlights the consistent temporal pattern where the majority of the *A. barbadensis* population migrates from northern rural areas in the rainy season (approximately September to February), to more southerly urban areas in the the dry season (approximately March to August).

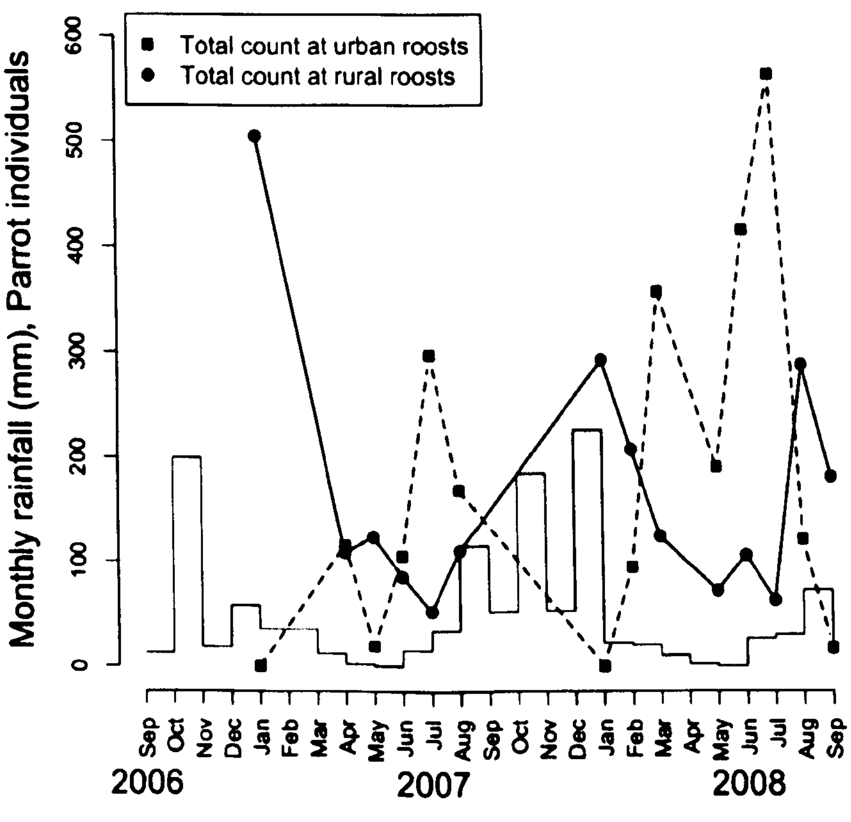

Figure 4.3. Monthly rainfall totals recorded at BOPEC and the number of *Amazona barbadensis* individuals attending roosts in urban and rural areas on Bonaire, Netherlands Antilles. Seasonal dry summers are evident from the rainfall bars, which correspond to lower count totals in rural roosts but higher count totals in urban roosts.

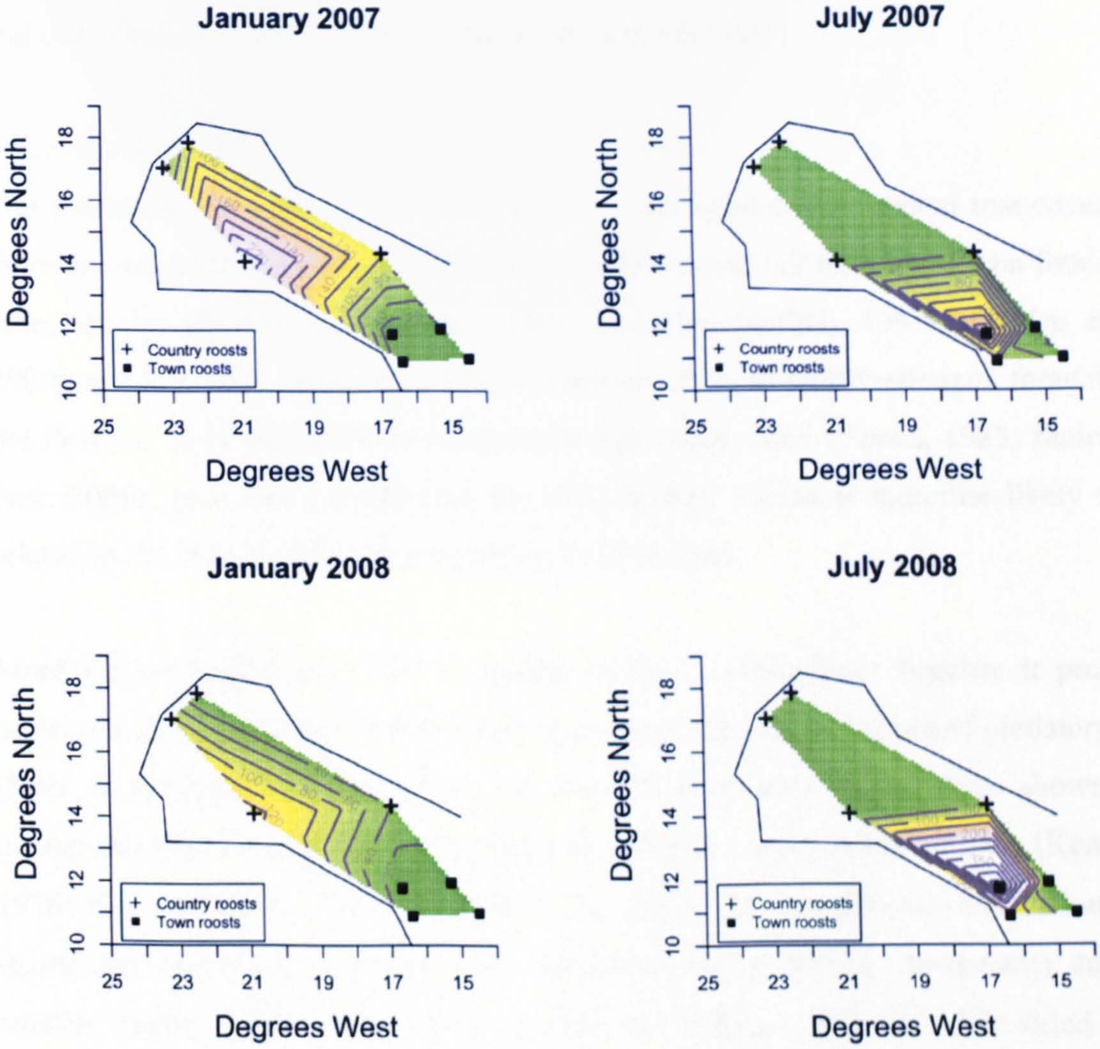

Figure 4.4. Contour plots of temporal variation in *Amazona barbadensis* abundance at each of the four rural and four urban roost sites. The similarity between these plots from January and July, 2007 and 2008 highlights the temporal pattern. The plots use terrain colours to represent the abundance of *A. barbadensis*. Green being areas of low abundance and brown and then white peak tops representing higher *A. barbadensis* numbers.

4.4. DISCUSSION

4.4.1. OVERVIEW

In this study I have demonstrated that a range of factors correlate with the spatial and temporal distribution of *A. barbadensis* on Bonaire. With respect to the questions posed in the methods: *A. barbadensis* abundance does correlate with habitat structure (Q1) and other bird species (Q2), the latter being a stronger relationship (Q3). A large proportion of the *A. barbadensis* population does move between urban and rural roost sites (Q4), and this is correlated with the previous month's rainfall (Q5).

4.4.2. SPATIAL DISTRIBUTION

The abundance of parrots is greater in more mature habitats (i.e. greater tree coverage, taller and larger trees). Associations between parrots and tall trees have been found for other species (Rowley & Chapman, 1991; Enkerlin-Hoeflich, 1995; Marsden et al., 2000), and like other Amazon parrots, *A. barbadensis* is primarily arboreal, foraging on the flowers, fruits and seeds of tree species and candle cacti (Voous, 1983; Juniper & Parr, 2003); pers. obs.). Preference for more mature habitat is therefore likely to be related to the improved foraging available in these areas.

More mature habitat may also be preferred by *A. barbadensis* because it provides protection from predators. Amazon parrots are prey for various species of predatory bird (Sanz & Rodríguez-Ferraro, 2006). Studies on other bird species have shown that greater structural complexity of habitat can result in lower predation rates (Kenward, 1978; Yue-Hua & Yu, 1994; Berkeley et al., 2007). On Bonaire, the crested caracara (*Caracara cheriway*) is resident, the peregrine falcon (*Falco peregrinus*) and the smaller merlin (*Falco columbarius*) are winter migrants, and the white-tailed hawk (*Buteo albicaudatus*) has been extirpated (Voous, 1983). Given that predation pressure is probably only seasonal under the current conditions and may never have been intense, this predator protection explanation for mature habitat preference may not be critical.

While much of Bonaire is vegetated, habitat quality (for *A. barbadensis*) over most of the island is low, as characterised by low tree coverage, fewer tall and larger trees (Figure 4.2.b). This is due to habitat degradation resulting from early colonists who removed the majority of trees and introduced feral goats (De Freitas, 2005). The latter have subsequently prevented the regeneration of many species, as is typical for many island ecosystems (De Freitas, 2005; Cruz et al., 2009). There are few *A. barbadensis* nests in areas of low habitat quality (Figure 4.2.b). Where there are nests, productivity is greater in areas where particular trees providing food resources, such as calabash (*Cresentia cujete*) and mesquite (*Prosopis juliflora*), are abundant (Chapter III). Habitat degradation and the resulting low quality habitat (as defined above) may therefore limit the distribution of *A. barbadensis* either through nest site limitation or food resource availability.

A. barbadensis has a fairly widespread distribution over Bonaire but at low abundances (Figure 4.2.a). This is a conservation concern because this population is by definition already limited by the size of the island. If the large areas of low quality habitat were restored then we might expect an increased carrying capacity for *A. barbadensis* on the island. Addressing the issue of habitat degradation through goat eradication and habitat restoration would probably benefit the *A. barbadensis* population and therefore be a worthwhile long-term conservation management strategy. However identifying short-term methods to enhance habitat quality locally would probably be of greater benefit for conservation initially, for example the provision of nest boxes and food supplementation have been key components in the successful conservation of various critically endangered species on Mauritius (Jones, 2005).

The distributions of *A. barbadensis* and possible competitors follow very similar patterns (Figures 4.2.a and b). Along the gradient of habitat quality, competitor abundance is more uniform than that of *A. barbadensis*. In high quality areas, *A. barbadensis* benefits disproportionately from increased tree coverage, more tall and large trees. In low quality areas the abundance of *A. barbadensis* and possible competitors decreases, but less so for the possible competitors. This suggests that parrots have more specialised habitat requirements and that possible competitor species experience fewer, or less intense, limits in areas of low quality habitat.

The relatively coarse resolution at which these patterns were determined, and the lack of experimental manipulation of any species means that it is not possible to conclude whether or not competition is occurring. Although the distributions and food resources of *A. barbadensis* and the possible competitors overlap, their niches are likely to be different (possibly behaviourally) to allow them to exploit the same food resource (MacArthur, 1958; Holmes et al., 1979). The differences in relative abundance between the species groups in high and low quality areas could be the result of these niche differences; *A. barbadensis* may have a competitive advantage in mature habitat whereas the other species are more competitive in low quality areas.

4.4.3. TEMPORAL DISTRIBUTION

A large proportion of Bonaire's parrot population move between urban and rural roosts depending on the previous month's rainfall. The effect of rainfall on the xerophytic rural environment is profound and the landscape of grey exposed tree bark transforms to a relatively lush green in a matter of days. When there has been little or no rain, the parrots migrate to roosts near the urban areas in which they forage (pers. obs.). Gardens and public spaces in urban areas contain native and exotic fruit trees, which in many gardens are irrigated. Consequently, urban areas on Bonaire can become a good food source for *A. barbadensis* in dry periods. Seasonal migrations have been observed in several other parrot species and these are also believed to be in response to food availability (Saunders, 1980; Snyder et al., 1987; Drechsler, 1998; Karubian et al., 2005; Manning et al., 2007). However, although there are occasional large trees, the overall habitat structure in urban areas does not match that which parrots were associated with in the analysis presented above, i.e. greater tree coverage, taller and larger trees. Therefore, the benefit of improved foraging in urban areas during dry periods appears to outweigh the benefit of staying in areas of more mature habitat.

The proportion of the *A. barbadensis* population that migrates to urban areas is considerable (e.g. 560 of an estimated 650 birds were observed at urban roosts in July 2008). These individuals are apparently non-breeders as their time budget and behaviour are very different to that of breeders (pers. obs.). Large non-breeding contingents have been observed in several other parrot populations and are a conservation concern with endangered species (Snyder et al., 1987; Beissinger & Bucher, 1992a; Beissinger & Bucher, 1992b; Munn, 1992; Kyle, 2005). The low breeding effort of the critically endangered Puerto Rican Amazon (*A. vittata*) was identified as a cause of slow population growth (Beissinger et al., 2008). In Chapter II I estimated that only approximately 22% of the *A. barbadensis* population on Bonaire breeds in a given year. Determining and ameliorating the factors limiting the number of breeding pairs for these *Amazona* species could increase their population growth which may be crucial following extreme weather events such as hurricanes in Puerto Rico or droughts in Bonaire.

Nest-site limitation was believed to cause the large non-breeding contingents seen in other parrot populations (Snyder et al., 1987; Beissinger & Bucher, 1992a; Beissinger & Bucher, 1992b; Munn, 1992; Kyle, 2005). The provision of nest boxes increased the number of breeding pairs in three species (Beissinger & Bucher, 1992a; Munn, 1992). Nest-site limitation may occur on Bonaire given the extent of historic and recent habitat degradation. Historical tree felling has reduced the number of large trees that might have provided nest sites and more recently poachers have cut nest trees open to extract chicks, rather than use former, less damaging, techniques (B. Frans, pers. comm.). In the absence of a nesting opportunity, non-breeding adult birds would not be constrained to stay near nest site and could therefore exploit the better foraging in urban areas.

The seasonal migration of parrots to urban areas leads to two conservation concerns. Firstly this behaviour causes a parrot-human conflict because the loss of fruit from people's gardens is attributed to these highly visible birds. This conflict is a serious issue in several areas and one that threatens to undermine other community-based conservation initiatives (Bucher, 1992; Graham et al., 2005; Caribbean Parrot Working Group 2009, pers. comm.).

A second concern is that moving to urban areas may expose parrots to increased mortality from collisions with vehicles and house windows (three and six cases observed in 2008 and 2009 respectively). If the migrating contingent of the *A. barbadensis* population experience greater mortality in urban areas than they would have had they stayed in rural areas, then the cues that attract the parrots to urban areas could be described as an ecological trap (Battin, 2004).

4.4.4. CONCLUSION

This study shows that a range of factors are likely responsible for the spatial and temporal distribution of *Amazona barbadensis* on Bonaire. Parrots show a preference for greater tree coverage, taller and larger trees. Habitat degradation equates to poor quality habitat for *A. barbadensis* and the overall lack of high quality areas could potentially limit their population size. Throughout their range, parrots overlap with three other bird species, but further study would be needed to determine the extent of competition. A large proportion of the *A. barbadensis* population migrates between urban and rural areas and this correlates with rainfall patterns. In dry periods many apparently non-breeding birds move from rural to urban areas. Following rainfall these birds return to rural areas.

Chapter V

NEST SITE SELECTION AND LIMITATION

5.1. INTRODUCTION

Ecology describes the fascinating multitude of connections between organisms and their environment. The abundance and distribution of every species is a reflection of numerous biotic and abiotic interactions (Morris, 2003). Niche theory provides a framework with which we can attempt to understand this complexity (Pulliam, 2000). Within their niche individuals distribute themselves in order to obtain the best resources available and maximise their survival and reproduction (Fretwell & Lucas, 1969; Southwood, 1977; Parker & Sutherland, 1986). Examining these patterns of habitat use through the development of resource selection functions (RSFs) can enable the prediction of an organism's distribution and abundance (Boyce & McDonald, 1999).

Across different taxa, nest site selection has been shown to have profound implications for an individual's fitness (Nilsson, 1984; Morris, 1991; Martin, 1995; White Jr et al., 2001; Eggers et al., 2006; Warner & Shine, 2007). Many bird species are dependent on specific nesting sites such as cliff ledges, burrows or cavities (Jackson & Tate, 1974; Cade & Bird, 1990; Snyder et al., 2000; Crawford et al., 2007)), and the availability of such nest sites often limits populations (Beissinger & Bucher, 1992a; Sedgwick & Knopf, 1992; Heinsohn et al., 2003; Crawford et al., 2007).

In several studies, areas of greater natural cavity availability have been shown to correlate with higher densities and a greater diversity of cavity-nesting birds (Legge et al., 2004; Diaz et al., 2005; Smucker et al., 2005). Furthermore, forest management resulting in a reduction of nest cavities is associated with a reduction of cavity-nesting birds (Raphael & White, 1984; Hobson & Schieck, 1999). However, the best evidence for cavity limitation comes from experimental nest box provisioning studies, where an increase in cavities increases the number of breeding birds (Brawn & Balda, 1988; East & Perrins, 1988; Gustafsson, 1988; Garcia-Navas et al., 2008).

Use of nests boxes by a species does not automatically indicate the population was limited by its access to nest sites. Tawny owls (*Strix aluco*) in managed British woodlands readily accepted boxes to the extent that within four years the total breeding population in the study (40 pairs) were using boxes despite the availability of natural cavities (Petty et al., 1993). Utilisation of a particular range of nest site characteristics at any given time may not reflect a species' true preferences but rather its preference under the given circumstances. In the absence of predators, many species use nests with more varied characteristics (Newton, 1998; Eggers et al., 2006). Similarly in North America, native eastern bluebirds (*Sialia sialia*) were constrained to relatively small cavities in the presence of introduced starlings (*Sturnus vulgaris*) but used a wide range of nest sites in areas without starlings (Pinkowski, 1976). There are, however, common environmental variables that impact quite generally on cavity nest selection. These include greater predation on lower nests, correspondingly greater competition for high nests. Similarly, predation also generates a preference for small entrance sizes and deeper nests (Nilsson, 1984; Belthoff & Ritchison, 1990; Wesolowski, 2002).

Investigating nest site preference and limitation in parrots is important because parrots are one of the most at risk groups of organisms on the planet (Bennett & Owens, 1997; Snyder et al., 2000; Juniper & Parr, 2003) Almost all parrots are secondary cavity nesters which predisposes them to be highly sensitive to habitat loss and natural pressures that constrain cavity use, e.g. predation or competition (Snyder et al., 2000). Moreover, the chicks of many species are harvested using destructive techniques including tree felling, compounding the problem (Wright et al., 2001; Pain et al., 2006). Several species are dependent on specific tree or palm species in which suitable cavities can be found and once established, breeders often show strong nest site fidelity (Garnett et al., 1999; Heinsohn & Legge, 2003; Berkunsky & Reboreda, 2009). Fortunately, parrots respond to the provision of nest boxes, which can be better protected from predators, but their acceptance of boxes may take many years (Sanz et al., 2003; Malham, 2007).

While adult survival is believed to be high in many parrot species (Rowley & Chapman, 1991; Brouwer et al., 2000; Snyder et al., 2000), cavity quality is likely to be important for breeding individuals and their offspring which are at risk from predation from either natural or introduced species (Snyder et al., 2000; Stoleson & Beissinger, 2001; Engeman et al., 2006; Koenig et al., 2007). Parrots may also face inter and intra-specific competition for nesting sites and as a consequence, infanticide (Snyder et al., 1987; Beissinger et al., 1998; Heinsohn & Legge, 2003). Intra-specific competition for nest sites may be so intense as to lead to female mortality, although the interaction is usually less escalated and is resolved through vocalisations and displays (Snyder et al., 1987; Heinsohn & Legge, 2003; Murphy et al., 2003).

In this study I describe the nest sites used by the yellow-shouldered Amazon parrot (*A. barbadensis*), and I investigate the availability of unused but apparently suitable cavities across different habitats on Bonaire. By comparing the characteristics of used and unused cavities, I generate resource (nest site) selection functions to characterise attributes of cavities preferred by *A. barbadensis* (Boyce & McDonald, 1999). I also experimentally increase the availability of nest sites by repairing former nests and providing nest boxes to examine whether the population is nest site limited.

There are several conservation benefits that arise from knowing how the parrots choose nest cavities. Several parrot populations are suspected to be nest site limited (Munn, 1992; Heinsohn et al., 2003; Sanz et al., 2003), and such limitation would constrain population growth. Yet, although parrot nest sites have been described in several studies worldwide (Nelson & Morris, 1994; Rodriguez-Estrella et al., 1995; Marsden & Jones, 1997; Sanz, 2006), little research has been conduced on the extent of available but unused cavities (Lanning & Shiflett, 1983; Enkerlin-Hoeflich, 1995; Legge et al., 2004), and even fewer have examined how nest site dimensions may influence nest site selection (Marsden & Jones, 1997; Manning et al., 2004). Therefore, understanding parrot nest site use and preferences is relevant for conservation, particularly as parrots inhabit some of the most threatened global ecosystems and are exposed to habitat destruction and degradation. The specific objectives of this study were to determine: 1. The dimensions of cavities used by *A. barbadensis* on Bonaire. 2. The dimensions of unused cavities on Bonaire. 3. The dimensions of cavities that are most important for their selection. 4. Whether *A. barbadensis* is limited by nest site availability.

5.2. METHODS

5.2.1. STUDY AREA AND SPECIES

This study was conducted on Bonaire, an oceanic island (288km2) of the Netherlands Antilles. Bonaire is in the Southern Caribbean Sea between 68° 11' - 68° 25' West and

12° 1' - 12° 9' North (Figure 4.1). The island has an average annual temperature of 28°C and receives low, irregular and localised rainfall. The average annual precipitation is 463mm, of which 51% falls in October, November and December. The xerophytic vegetation is highly heterogeneous and has been degraded dramatically since European colonisation and the introduction of free-ranging goats (De Freitas, 2005). Further habitat degradation results from poachers cutting access holes into tree nests to remove parrot chicks.

A. barbadensis is a medium-sized parrot (275-365g). Its distribution on Bonaire is widespread but excludes the southern quarter of the island, which is largely a windswept wetland area with few trees. Breeding typically takes place between May and August, and nests are found in clusters or in isolation across the island, north of Kralendijk. Amazon parrots are secondary cavity nesters and on Bonaire *A. barbadensis* nests in tree and rock cavities. The latter are found either in large boulders or on cliff faces (~20m high), in either heterogeneous volcanic or limestone formations (De Freitas, 2005). During the breeding season, pairs exclude other parrots from the immediate vicinity of their nest.

5.2.2. CAVITY DESCRIPTION AND AVAILABILITY

5.2.2.1. Definition of terms

Available cavities are defined here as any hole in a cliff or tree. An available cavity may or may not be suitable for use by *A. barbadensis*; a suitable cavity may or may not be used by *A. barbadensis*. In this study, seven cavity dimensions (see below) are used to describe all cavities. For an unused available cavity to be considered suitable every one of the dimensions measured must be within the range used by *A. barbadensis* (as observed when describing nest sites). For ease of reading the term "nest" is used interchangeably with the definition "available, suitable and used cavity".

5.2.2.2. Nest searches and description

I conducted structured nest searches with the help of volunteers each year. Nests were located by tracking pairs exhibiting nest-prospecting behaviour, or by opportunistic searches of cliffs and trees. Possible nests were inspected for activity either by eye or with digital cameras. I recorded/measured the following nine characteristics at each nest (and later at every cavity): cavity type (tree/cliff), height above ground (measured as a plumb line from the cavity entrance to the ground (cm), entrance height (cm), entrance width (cm), entrance hole area (cm^2), internal vertical depth (cm), internal horizontal length (cm), cavity floor area (cm^2) and habitat type (following (De Freitas, 2005). Tree species and tree diameter at breast height (cm) were also recorded/measured where appropriate. The distribution of tree nests among different habitats was examined using a chi-squared test.

5.2.2.3. Unused cavity searches and description

Searches for available cliff cavities were conducted on five randomly selected 100m sections of cliff. All searches were conducted with the help of volunteers. An initial selection was made whereby cavities with entrance dimensions (height and width) outside the observed range used by *A. barbadensis* ± 20% were not measured (see below). The same nine characteristics (above) were measured.

At each of the five random locations and a further 31 known nest sites, I also searched a four hectare (200 x 200m) quadrat for tree cavities. These quadrats were centred on the nest or mid point of the random cliff and followed the cardinal directions.

5.2.2.4. Determining cavity availability

I calculated the number of available, suitable but unused cavities by selecting only those cavities for which all seven numeric measurements were within the range used by parrots ± 20%. This selection removed unnecessary sampling of inaccessible cavities that *A. barbadensis* could not fit into and large cavities, which would not represent nests. The depth of long horizontal shaped nests may be zero. Similarly, vertical shaped nests may not have large length measurement. It was therefore possible for a shallow unused cavity with limited length to be considered suitable when it would not be. Consequently, the combination of internal length and depth was reassessed in three subsets of selected cavities with depths of <34cm (the minimum observed tree nest depth), <20cm and <10cm. Cavities from each subset with lengths less than that observed in nests of similar depth were eliminated.

5.2.3. RESOURCE SELECTION FUNCTION (RSF) MODEL OF NEST SITE SELECTION

I used RSFs to quantify the relative importance of specific nest dimensions (Boyce & McDonald, 1999). This method applies binary logistic regression (GLM) to the data on used (1) and unused (0) cavities as a function of the nine nest variables. All models were simplified with a backwards, stepwise model reduction.

5.2.4. FORMER NEST REPAIR AND NEST BOX PROVISION

Many deep tree nests are cut open by poachers in order to extract the chicks. To examine whether parrots would respond to an increase in the number of available cavities I repaired 10 such former nest trees. I also provided 12 boxes (built within observed nest dimensions) across the north of the island in areas used by parrots. These boxes were positioned in trees (6) and on cliff faces (6).

5.3. RESULTS

5.3.1. CAVITY DESCRIPTION AND AVAILABILITY

5.3.1.1 Characteristics of cavities used as nests

A total of 58 nests were found during the course of this study. The characteristics of these used cavities are described in Table 5.1. The dimensions reflect the fact that tree nests were typically vertical cavities within the tree trunk whereas cliff nests were more varied in shape and consequently in internal length. Tree and cliff nests were found in 10 different habitat types (Table 5.2). The composition of the surrounding habitat may influence a cavity's suitability, however external nest area characteristics are not dealt with here. Tree nests were particularly abundant in two habitat types: *Haematoxylon-Croton* and *Prosopis-Casearia*. The former is dominated by brasilwood (*Haematoxylon brasiletto*) with rock sage (*Croton flavens*) being the second most dominant species. The latter habitat type is dominated by mesquite (*Prosopis juliflora*) and yellow wood (*Casearia tremula*). The distribution of tree nests differed significantly among habitat types ($\chi^2 = 34.77$, $df = 9$, $P < 0.001$). The majority (31 of 49) of unused tree cavities were also found in the *Prosopis-Casearia* habitat. Tree nests were found in 12 different species of tree and these are described in Table 5.3.

5.3.1.2. Description of unused cavities

The plots in Figure 5.1 show the range of observed dimensions for both used and unused tree and cliff cavities. The lower limit to the range of entrance heights and widths results from the sampling regime, whereby cavities were not considered if they were 20% outside the maximum or minimum measurement observed in nests. Most nests are found at the lower end of the entrance height, width and area range for both trees and cliffs. A greater range in depth is seen from tree cavities than from cliff cavities and this reflects the fact that all tree nests are vertical in orientation, whereas cliffs may be shallow but extend a long way into a cliff horizontally. This is illustrated again in the final plot where many cliff cavities have considerably larger floor areas than those in trees.

5.3.1.3. Cavity availability

Cavity searches were conducted on a total of 500m of cliff varying in height from 8 to 25m. Measurements were taken from 105 cliff cavities (Table 5.2), eight of which had dimensions within the range used by *A. barbadensis* ± 20%; thus these cavities were considered suitable but unused.

The tree cavity searches of four-hectare quadrats, conducted at five random locations and 31 nest sites, yielded a total of 144 hectares, 122.5 of which were unique. Overlap of the four-hectare quadrats occurred where nests were close to their neighbours. As with used cavities, the majority (70%) of available and suitable cavities were found in *Prosopis – Casearia* habitat (Table 5.2). Available and suitable cavities were found in five identified tree species, several unidentified tree species, and one cactus (Table 5.3). Use of the known tree species by nesting parrots has been observed during this study and use of the cactus has been reported previously (Mellink & Molina, 1984).

5.3.2. RSF MODEL OF NEST SITE SELECTION

I used 39 tree and cliff nests and 68 unused available tree and cliff cavities to parameterise the resource selection function model describing *A. barbadensis* nest sites on Bonaire. Four dimensions were either statistically significant or approached significance: entrance height ($z = 1.74$, $df = 1$, $P = 0.058$), entrance area ($z = -2.78$, $df = 1$, $P < 0.001$), depth ($z = 2.56$, $df = 1$, $P < 0.01$), and cavity floor area ($z = 3.42$, $df = 1$, $P < 0.001$). The plots in Figure 5.2. show the probability of cavity use for each variable, controlling for the other three dimensions. *A. barbadensis* preferred cavities with higher entrances but there was much stronger selection for cavities with small entrance areas. Deeper cavities were preferred as were nests with greater floor area. The strength of these last two relationships was similar.

Table 5.1. Cavity dimensions of tree, cliff and summed nests used by *A. barbadensis* on Bonaire, Netherlands Antilles, (2006 – 2008), (mean ± SD (range), n). Tree nests are typically lower than cliff nests yet the entrance dimensions of both types are similar. Tree nests tend to be vertical whereas cliff nests may also be horizontal and consequently have larger cavity floor areas.

Cavity type	Cavity height (cm)	Entrance height (cm)	Entrance width (cm)	Entrance area (cm^2)	Internal depth (vertical; cm)	Internal length, (horizontal; cm)	Cavity floor area (cm^2)
Tree	189.30 ± 88.00	19.30 ± 10.11	13.13 ± 5.22	252.08 ± 158.35	99.85 ± 61.51	27.07 ± 9.00	668.47 ± 372.81
	(77 - 405), 26	(9 - 47), 26	(6 - 29), 26	(72 - 658), 26	(34 - 290), 26	(15 - 40), 15	(255 - 1292), 15
Cliff	663.00 ± 354.10	19.19 ± 14.29	15.42 ± 6.37	294.68 ± 231.79	32.90 ± 32.59	89.97 ± 59.00	2471.96 ± 1864.90
	(170 - 1700), 32	(8 - 77), 31	(8 - 36), 32	(88 - 1008), 31	(0 - 100), 30	(18 – 300), 30	(270 - 6600), 26
All cavities	450.66 ± 357.85	19.25 ± 12.45	14.40 ± 5.95	275.25 ± 201.08	63.98 ± 58.43	69.00 ± 56.74	1812.15 ± 1730.83
	(77 - 1700), 58	(8 - 77), 57	(6 - 36), 58	(72 - 1008), 57	(0 - 290), 56	(15 - 300), 45	(255 - 6600), 41

Table 5.2. Distribution among habitat types of tree and cliff cavities, used or unused by *A. barbadensis* (2006 – 2008), on Bonaire, Netherlands Antilles.

Habitat type [a]	Tree nests	Cliff nests	Hectares searched	Unused available tree cavities around nests	Unused available tree cavities around random cliffs	Unused available cliff cavities	Total unused cavities found	Suitable but unused tree cavities	Suitable but unused cliff cavities
Anthropogenic	2	0	4	1	NA	NA	1	1	
Aristida - Jatropha	0	6	16	1	0	36	37		5
Caesalpinia –Metopium	0	3	8	1	0	22	23		1
Croton - Prosopis	1	0	4	0	NA	NA	0		
Eragrostis - Cyperus	3	0	12	12	0	32	44	3	2
Erithalis - Bourreria	0	5	12	0	NA	NA	0		
Haematoxylon – Casearia	4	7	24	0	NA	NA	0		
Haematoxylon –Croton	8	1	16	3	0	11	14	2	0
Prosopis – Casearia	8	8	40	31	0	4	35	14	0
Prosopis - Opuntina	0	2	8	0	NA	NA	0		
Total	26	32	144	49	0	105	154	20	8

[a] Genus of the dominant and second most dominant species, following (De Freitas, 2005)

Table 5.3. The number of nests used by *A. barbadensis*, and suitable but unused cavities in different species of tree, and their dimensions on Bonaire, Netherlands Antilles, (2006 – 2008).

Common name	Family	Species	Nest tree DBH [a], mean (range), (cm)	Nests	Suitable but unused cavities
Cherry	Boraginaceae	*Bourreria succulenta*	NA[b]	1	
White Gum Tree	Burseraceae	*Bursera bonairensis*	45	1	
West Indian Birch	Burseraceae	*Bursera simaruba*	52.3 (38 – 67)	4	1
Dividivi	Fabaceae	*Caesalpinia coriaria*	37 (28 – 46)	2	
Palu di Lora	Capparidaceae	*Capparis coccolobifolia*	30.7 (23 – 36)	3	
Black Willow	Capparaceae	*Capparis cyanphallophora*	42.7 (31 - 51)	5	5
Kadushi	Cactaceae	*Cereus repandus*			1
Calabash	Bignoniaceae	*Crescentia cujete*	117	1	2
Lignum Vitae	Zygophyllaceae	*Guaiacum officiale*	48.5 (30 - 67)	2	
Manchineel Tree	Anacardiaceae	*Metopium brownei*	31.7 (27 - 34)	4	1
Mesquite	Mimosaceae	*Prosopis juliflora*	28 + NA[b]	2	3
West Indian Satinwood	Rutaceae	*Zanthoxylum flavum*	140	1	
Unidentified					7
Total			41.1 (23 - 67)	26	20

[a] Diameter at breast height

[b] Fallen or partially fallen trunk prevented DBH measurement

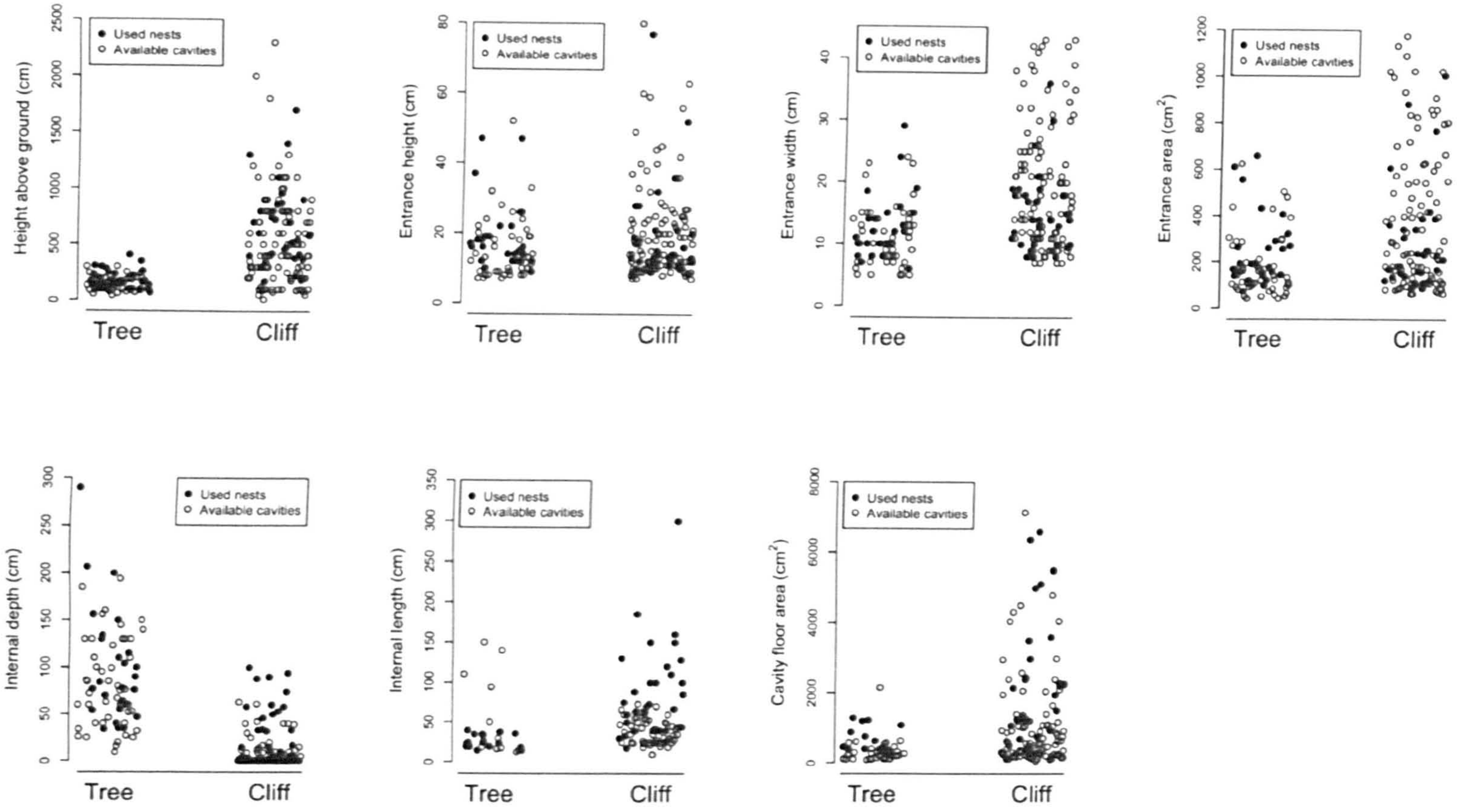

Figure 5.1. Dimensions of used (filled circles) and unused (unfilled) cavities found in trees and cliffs on Bonaire, Netherlands Antilles. Tree cavity height above the ground is limited by the vegetation height, which rarely exceeds 4m. Minimum internal depths in tree nests are greater than in cliff nests as they lack internal length whereas cliff cavities can extend 3m horizontally.

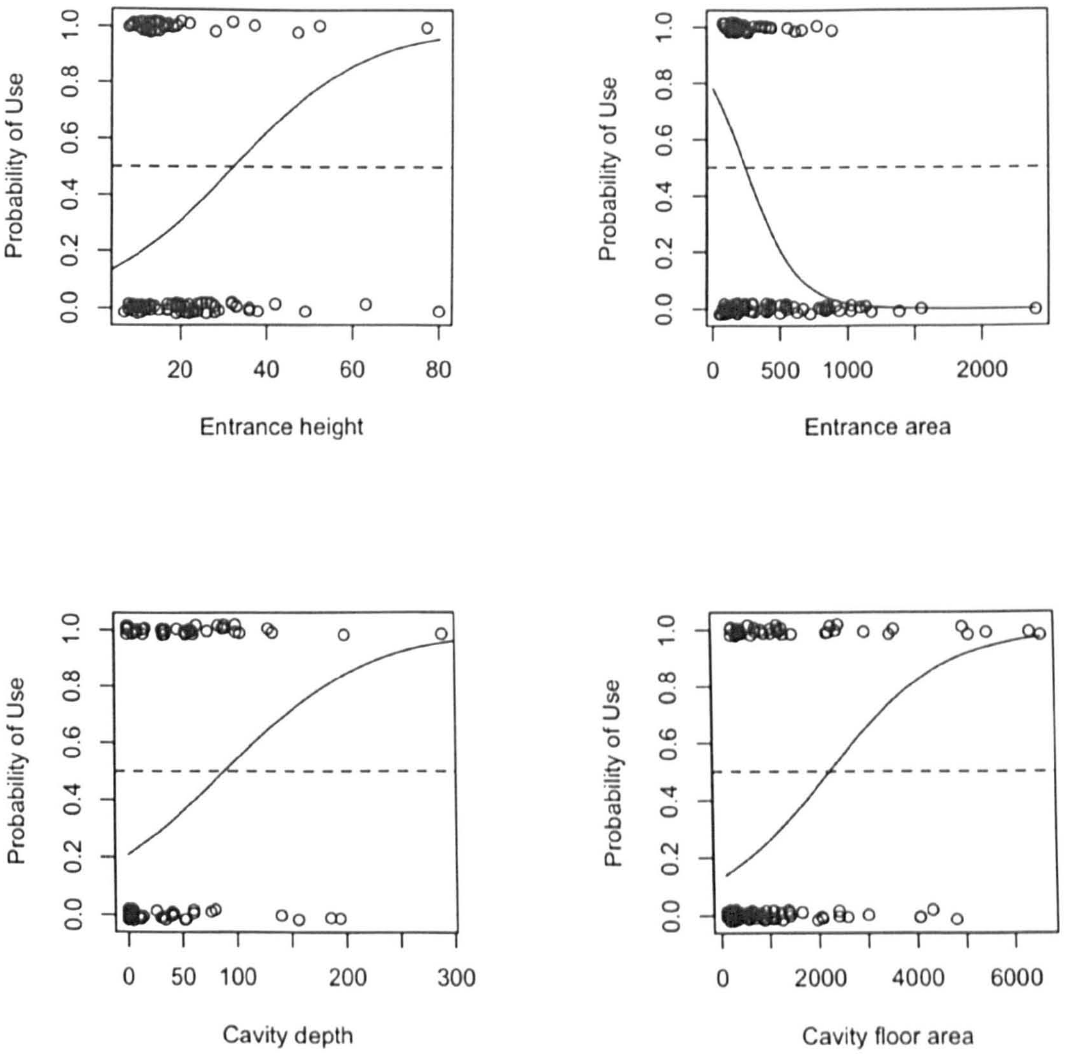

Figure 5.2. Probability (solid line) of cavity use in relation to: entrance height, entrance area, cavity depth and cavity floor area. Points are offset slightly to reveal multiple similar data. The dashed line represents 50% probability, thus in C, for example, a cavity with a depth of 80cm has a 50% probability of being used.

5.3.3 FORMER NEST REPAIR AND NEST BOX PROVISION

Eggs were laid in three of the 10 repaired former nest trees but no nest box was used during the course of this study. The identity of the pairs could not however be confirmed and so it remains uncertain whether these birds were non-breeders in previous years or whether they were breeding pairs moving from unknown nests.

5.4. DISCUSSION

5.4.1. OVERVIEW

In this study, I have described the cavity characteristics used by *A. barbadensis* on Bonaire. I have demonstrated that there are unused cavities of suitable dimensions in different habitat types, and by using data on used and available cavities I produced a resource selection function model describing parrot nest site preference, indicating entrance height, entrance area, cavity depth and cavity floor area as critical in cavity selection. Finally, I found that repaired former nest trees were reused immediately but nest boxes that were erected during this study were not.

5.4.2. NEST SITE CHARACTERISTICS

Overall there was a large range in the nest site dimensions used on Bonaire, as has generally been found in other *Amazona* (Snyder et al., 1987; Enkerlin-Hoeflich, 1995; Seixas & Mourao, 2002). Two continental species are notable exceptions: the lilac-crowned Amazon (*A. finschi*) and the blue-fronted Amazon (*A. aestiva*) both of which show much less variation in nest entrance dimensions (Renton & Salinas-Melgoza, 1999; Castillo & Eberhard, 2006). Historically, on the oceanic island of Bonaire *A. barbadensis* has probably not been tightly constrained to selecting only those cavities with small entrances because of the lack of natural nest predators. However, *A. barbadensis* is now exposed to predators that have been introduced to the island, the most important of which are probably cats, which predate chicks from nests with relatively large entrances (pers. obs.).

A. barbadensis on Bonaire nests in cliffs and various tree species, among a variety of habitat types. This is fairly typical of *Amazona* species, several of which also breed in a range of different trees and among different habitats (Enkerlin-Hoeflich, 1995; Seixas & Mourao, 2002; Castillo & Eberhard, 2006). Interestingly the exceptions are other populations of *A. barbadensis* where on Margarita 85% of the population nest in a single tree species (*Bulnesia arborea*) and on La Blanquilla 98% nest in another, different tree species (*Guaiacum officinale*; Rodríguez-Ferraro & Sanz, 2007). Whether the almost exclusive use of particular trees on these islands represents a preference or a limitation is unclear as the habitats are different, and unused cavities on each island were not described.

5.4.3. AVAILABILITY OF SUITABLE CAVITIES

As a result of numerous cavity searches, I found 28 unused cavities of suitable dimensions. Given the extent of cliff and un-sampled habitat this result suggests the availability of suitable cavities is not severely limiting for *A. barbadensis* on Bonaire. Other studies on *Amazona* species have also found suitable but unused cavities around nest sites (Enkerlin-Hoeflich, 1995; Rodríguez-Ferraro & Sanz, 2007). It may however be that some component of suitability is missing from the assessments that have been used by researchers so far. This is discussed further in section 5.4.5, below.

5.4.4. NEST SITE SELECTION

Through the analysis of used and available cavities, I produced a nest selection function comprised of four nest site dimensions (all $z > 1.74$, $df = 1$, $P \leq 0.058$): entrance height, entrance area, internal vertical cavity depth and cavity floor area. Competition and predation risk would be expected to result in a preference for smaller nest entrance areas (Pinkowski, 1976; Eggers et al., 2006), so the positive correlation between use and entrance height is a curious result. One possible explanation is that tall but narrow entrances are acceptable for parrots and their use reduces competition with other species, such as iguanas (*Iguana iguana*). Parrots are able to enter remarkably narrow nests, the minimum observed entrance width being 6cm (Table 5.1). Iguanas are abundant on the cliffs, use tree cavities and even share cavities with (successful) nesting parrots. However, narrow nest entrances, which may include a tunnel leading to the nest chamber, would be difficult for mature iguanas to navigate.

The entrance height result may also have been the consequence of a bias in the sampling methodology, because nest entrance dimensions were used in the field to initially determine whether or not to record measurements on a given cavity. Only cavities with entrance dimensions (height and width) within the range observed used by parrots ± 20% were measured, the sample of random nest cavity entrance height has an upper (and lower) limit. The majority of nests appear to be at the lower end of the entrance height range (Figure 5.2), yet the few high entrance nests have a strong influence on the selection probability. Thus, given the potentially biased sampling methodology, I would be cautious to draw too many conclusions on the ecological meaning of this result.

Entrance area was calculated by multiplying entrance height and width. Although some nest entrances may be large on one axis (tall and narrow, or wide but low) no nest entrance was large along both axes. Consequently the upper end of the size range for this measurement on available cavities was much greater in random cavities than in nests (Figure 5.2).

On Bonaire, the most likely nest predator, historically, would have been the white-tailed hawk (*Buteo albicaudatus*), which is now extirpated on the island. Other hawks (*Buteo sp.*) are known to predate nestlings of other *Amazona* species (Snyder et al., 1987). However, introduced domestic cats are abundant and they predate nests with sufficiently large entrances to allow access (pers. obs.). A preference for cavities with a combination of smaller entrance dimensions and deeper nest depth may reduce nest predation. Indeed, there was evidence in Chapter III of a (non-significant) negative relationship between nest entrance and brood size prior to fledging suggesting that even with a different range of predators there may be a fitness benefit from the selection of smaller nest entrances.

On Margarita, where the *A. barbadensis* breeding population increased from 26 pairs to 55 pairs in less than 10 years, the only reported change in nest sites was the use of lower and shallower nests (Sanz, 2006). Nest depth was identified an important determinant of nest site selection in this study, however a preference for higher nests was not. In studies of continental *Amazona* species, where the vegetation is much taller than it is on Bonaire, nest height above the ground is correspondingly higher (Enkerlin-Hoeflich, 1995; Renton & Salinas-Melgoza, 1999). Indeed, Enkerlin-Hoeflich (1995) found unused apparently suitable nests at lower heights than the used nests. The use of less preferred nest sites as a result of increased competition as the Margarita population has grown fits with established nest site selection patterns (Nilsson, 1984; Belthoff & Ritchison, 1990; Wesolowski, 2002).

Nests with more floor area may improve nest hygiene or reduce parasite loading. Chick faeces or dead siblings were not removed from cavities by adult birds and the smaller nests were unquestionably less hygienic (pers. obs.; we removed dead chicks during this study). Alternatively, large nests may benefit parents trying to allocate food to boisterous chicks. The combination of asynchrony and nest site shape may increase the risk of mortality to the smallest chick (R. Martin, pers. comm.). The preference of larger nests may therefore improve the provisioning of the entire brood. However in the earlier analysis (Chapter III) a positive correlation between cavity floor area and brood size prior to fledgling was only moderately supported.

5.4.5. USE OF REPAIRED NESTS AND NEST BOXES

In order to examine whether *A. barbadensis* was nest-site limited, nest boxes were installed in 12 parrot breeding areas and 10 former nest trees were repaired. Three repaired nests were used, but this result did not confirm that *A. barbadensis* is nest site limited because too few of the breeding population were ringed to confirm that the "new" breeders were not breeding elsewhere previously. The failure of the parrots to use nest boxes was not surprising because getting parrots to accept nest boxes is notoriously difficult (Sanz et al., 2003).

On Margarita, *A. barbadensis* first used wooden nest boxes four years after their installation, whereas all repaired nest trees were used in the same or the following season (Sanz et al., 2003). Similar behaviour has also been observed with the Puerto Rican Amazon (*Amazona vittata*; Snyder et al., 1987), which now nests in artificial nests made from plastic water pipes (White et al., 2005). The difficultly of getting parrots to accept nest boxes highlights our lack of knowledge of the way in which parrots locate and ultimately select nest sites.

Apparently suitable yet unused cavities have been identified in this and other studies (Enkerlin-Hoeflich, 1995; Rodríguez-Ferraro & Sanz, 2007). So why are these cavities not being used? It may be that key physical features were not recorded, for example, nest entrance surface texture that allows easy access. Alternatively, some feature other than the physical dimensions of a cavity may be important. Several researchers have noted either that their study species nested in clusters, or that social factors are probably important in nest site selection (Snyder et al., 1987; Gnam & Rockwell, 1991; Smith, 1991; Enkerlin-Hoeflich, 1995; Marsden & Jones, 1997; Garnett et al., 1999; Cameron, 2006). Yet in over 20 years, researchers have not made progress on this topic, which deserves further study. A better understanding of nest site selection would clearly be useful for species conservation and the protection of key areas.

5.4.6. CONCLUSION

This study showed that *A. barbadensis* on Bonaire nests in cavities with a range of dimensions and that this is largely typical of the genus. The availability of unused cavities did not appear to be limited, however physical measurements alone may not be adequate to define cavity suitability. A resource selection function model indicated that four nest dimensions are important in parrot nest site preference. This result may be useful for stimulating further research in other environments and may help guide future nest box design, potentially aiding experimental tests of nest site limitation. Former nest trees were re-used when repaired however the nest boxes provided were not. Overall, it is not possible to conclude whether nest sites are limited or not. Determining why apparently suitable nests are not used is critical for the correct assessment of nest site limitation, which has conservation implications. Key factors that demand further study in the context of population management include the cues used to detect available nest sites, further internal features that may influence cavity use and the social requirements of nesting parrots.

Chapter VI

CONSERVATION BONAIRE PROPOSAL

SUMMARY

Conservation Bonaire aims to be the first conservation and community-oriented tourism project on Bonaire, modelled after successful operations in Peru, Guyana, Borneo and other countries. Bonaire is remarkable among Caribbean islands because it still has considerable terrestrial and marine wilderness intact. However, these ecosystems are no longer pristine and continued degradation will undermine the economic benefit they can provide. Conservation Bonaire's approach will make Bonaireans partners in sustainable economic growth, and promote Bonaire globally as a leader in eco-tourism. Conservation Bonaire will:

- Develop sustainable tourism to benefit the local community and conservation,
- Facilitate research and the conservation of threatened ecosystems.
- Mitigate environmental impacts caused by residents and tourists on the island,
- Commit to strategic, long-term approaches that build local capacity

6.1. INTRODUCTION

6.1.1. BONAIRE

Bonaire is remarkable among Caribbean islands because it still has considerable terrestrial and marine wilderness intact. With a population of only 12,000 people, this small dry island of 288km^2 is a treasure trove of ecosystems. The Washington-Slagbaai National Park in the northwest covers approximately one fifth of the island and has good examples of the natural vegetation. Even outside the Park there are large areas where relatively little development has taken place. The flora and fauna of these arid wilderness areas are unique to the Southern Caribbean region and include endangered species such as the tree lignum vitae and the yellow-shouldered Amazon parrot.

Around the coast of the island are several saltpans, which are important feeding areas for migrant birds. Seabirds breed on the windward coast and further south in the two RAMSAR sites: Pekelmeer and Lac Bay. The former is one of only two breeding areas in the southern Caribbean for the Caribbean flamingo, Bonaire's national bird. The beautiful Lac Bay is an important area for feeding area for green, hawksbill and loggerhead turtles, and the mangroves that border the lagoon are critically important nursery grounds for reef fish.

The Marine National Park, which includes all coastal waters to a depth of 60m, is home to over 370 species of fish, and the three species of turtle (above) return to the island annually to breed. Established for over 30 years and a source of pride for Bonaire's proactive community, the park champions the motto "leading by example". Indeed Bonaire is recognised internationally for having some of the best-preserved reefs in the Caribbean. It is also a demonstration site for the International Coral Reef Action Network. With such early environmental awareness it is perhaps not surprising that Bonaire's progressive leaders revealed their ambition to become the first carbon neutral island country.

Bonaire's wilderness areas may appear to be in good condition; following rainy periods much of the island is green, and divers are happy (Scuba, 2008). However the function of the terrestrial and marine ecosystems is compromised, and if the pressure that humans put upon them continues, they will collapse. Degradation of the terrestrial ecosystem indirectly affects the marine ecosystem. In particular, loss of vegetation resulting from goats browsing leads to soil erosion and increased sediment reaching the reef. People also put pressure on the reef ecosystem directly. Recreational use has led to widespread physical damage, and the lack of adequate wastewater treatment has reduced water quality and fertilised algal growth.

Tourism is the largest industry on Bonaire but this is not managed in a sustainable manner at present. This is a major conservation concern but should also be an economic concern. Furthermore, the tourism industry is run largely by Europeans and Americans, and consequently there is a skewed income distribution among the population and increasing poverty. So not only is the heritage of the local population being degraded, but they are not benefiting financially from tourism. In fact, the tourism industry takes a paternal view of the local community epitomised by the ongoing "Smile" campaign, which encourages local people to smile at tourists.

Bonaire's diverse collection of ecosystems provides a range of services to the human population such as cultural benefits, food and climate regulation. Most of these ecosystem services are difficult to value but there can be no doubt that the aesthetic and recreational services (cultural) provided by the reef are of critical importance to Bonaire's economy. Over 74,000 overnight tourists holiday on the island annually. A further 250,000 people visit on cruise ships. Diving on the reef is the main reason that 60% of tourists visit the island (Tourism Corporation Bonaire, 2008). Even under the current situation the future of Bonaire's economy is profoundly dependent on the conservation of both terrestrial and marine ecosystems.

Eco-tourism is defined by the International Ecotourism Society (2009) as: "*Responsible travel to natural areas that conserves the environment and improves the well-being of local people*". Ecotourism is recognised as being among the fastest growing sectors in the tourism industry. Yet Bonaire's tourism industry does not attract or cater for eco-tourists. Nor has Bonaire's tourism industry taken advantage of the huge potential for terrestrial-based nature tourism. In the United States alone 48 million people were involved in birding in 2006 and those individuals spent a staggering $82 billion on their hobby (U.S.F.W.S.). Naturally, these individuals are not all spending their money on overseas nature-related travel but nonetheless the size of the market is seldom appreciated. Arrivals from the USA represent a 43% share of the tourist market on Bonaire. Globally this market is vast and if managed appropriately has the potential to boost sustainable economic growth on Bonaire.

6.1.2. REGIONAL CONSERVATION AND SUSTAINABILITY ISSUES

The Caribbean Sea region is recognised by numerous initiatives as a biodiversity hotspot; a threatened region of exceptionally diverse ecosystems (e.g. The Critical Ecosystem Partnership Fund). Bonaire's conservation and sustainability issues are representative of a global problem. To better understand the consequences of current changes to global ecosystems, former United Nation's Secretary General Kofi Annan launched a comprehensive scientific study called the Millennium Ecosystem Assessment (MEA). This initiative took place from 2001 to 2005 and involved the work of more than 1,360 experts worldwide. When evaluating scenarios for the future of the Caribbean Sea region (to 2050) this study found that: "Continued neglect of ecosystems could result in such degraded environments that the Caribbean would lose its tourism appeal and fishing stocks would collapse."

The assessment identified human impacts that directly affected the capacity of Caribbean ecosystems to provide services. These included: coastal land and sea use, sewage pollution, over-fishing, climate change, and the introduction of alien species. Ecological impacts resulting indirectly from human activities were also identified and included: urbanisation of coastal communities and high investment in unsustainable tourism.

Each of these above factors identified by the United Nations assessment is relevant to Bonaire. How Bonaire stands apart from other Caribbean islands is the positive and progressive attitudes within the Island Government. This is no doubt a result of the large and well-established conservation community and the high awareness of conservation issues within the local community.

6.2. CONSERVATION BONAIRE ORGANISATIONS AND THEIR OBJECTIVES

6.2.1. CONSERVATION BONAIRE OBJECTIVES

Conservation Bonaire will be an institution that brings together key components of the conservation and environmental movements.

The mission of Conservation Bonaire is:

"To develop strong relationships with other organisations and businesses on Bonaire so we may efficiently and effectively work together to develop sustainable tourism, study and conserve threatened ecosystems and mitigate environmental impacts caused by residents and tourists. To build local capacity through education and training; build the capacity of conservationists in the region through improved communications and networks, and raise global awareness of conservation and sustainability issues though strategic marketing of our approaches."

In order to achieve this mission Conservation Bonaire will function as an umbrella institution to four distinct organisations, each with its own purpose and goals. Conservation Bonaire will support and direct: Eco-Tourism Bonaire, Bonaire Conservation Volunteers, Conservation And Research Institute Bonaire, and Holistic Eco-Living Project. For simplicity the four organisations hereafter will be referred to collectively as "The Quad".

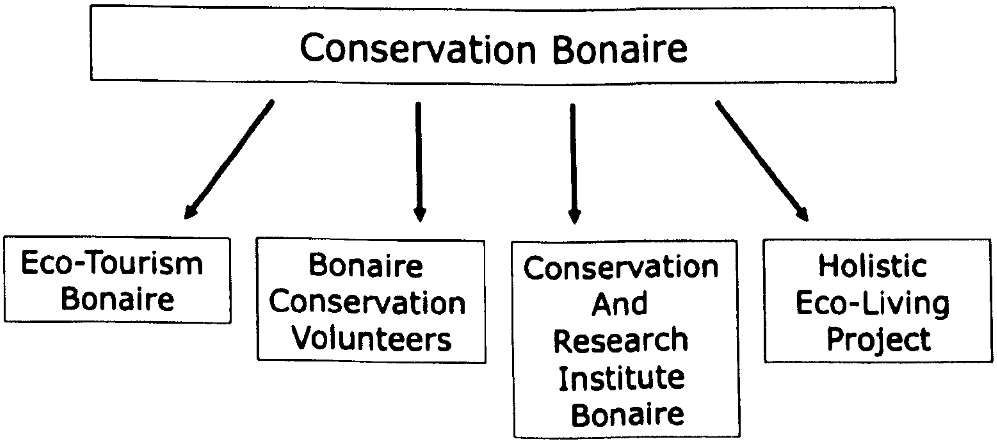

FIGURE 6.1. Conservation Bonaire as the umbrella institution above The Quad.

Biologists Sam Williams and Rhian Evans will lead Conservation Bonaire. Their wealth of relevant experience includes developing, guiding and managing sustainable tourism in South and Central America; the conservation of endangered animals and plants on several projects worldwide; and research in tropical, temperate and sub-Antarctic environments. Throughout the process of developing this proposal into a business plan and then executing it, Sam and Rhian will be supported by an advisory group of professionals with specialist expertise in these diverse areas.

6.2.2. ECO-TOURISM BONAIRE OBJECTIVES

Eco-Tourism Bonaire will be a non-profit business that supports community and conservation projects. Guests will stay in exclusive cabins at The Eco Lodge, which will be a best practice example of development with a low environmental impact. Guided activities available to guests and other tourists will provide intimate encounters with charismatic flagship species such as parrots, flamingos and turtles, and learning experiences about the wider terrestrial and marine ecosystems. The mission of Eco-Tourism Bonaire is:

> *"To develop sustainable tourism that supports the local community and the conservation of Bonaire's ecosystems. To facilitate local enterprise in the development of sustainable experiential tourism."*

6.2.3. BONAIRE CONSERVATION VOLUNTEERS OBJECTIVES

Bonaire Conservation Volunteers will be an organisation that recruits paying volunteers to Bonaire. Work programs of three weeks or more, will provide the opportunity for groups of up to 12 volunteers to experience a diverse range of conservation work including habitat restoration, community education and species research. The mission of the Bonaire Conservation Volunteers is:

> *"To provide labour and generate income for Conservation Bonaire organisations and to give volunteers empowering, positive and memorable experiences of conservation work."*

6.2.4. CONSERVATION AND RESEARCH INSTITUTE BONAIRE (CARIB) OBJECTIVES

CARIB will be a collection of resident and visiting conservationists, educators, community developers and scientists that build on the success of the Bonaire Parrot Project, which includes this PhD Research project and that of Rowan Martin. CARIB's work is arranged into five themes that will help present and structure its efforts (Figure 6.2). Each of these themes will be outlined below. CARIB's mission is:

> *"To develop rigorously assessed creative conservation approaches, conduct and facilitate outstanding scientific research, and to build regional capacity in these fields."*

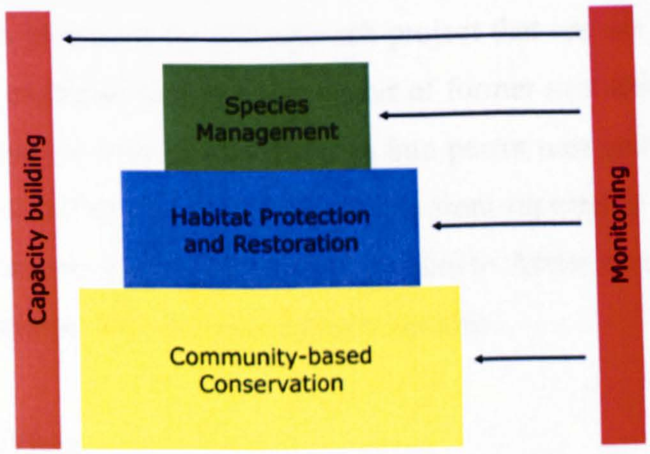

FIGURE 6.2. The five themes to be used by Conservation And Research Institute Bonaire in structuring its work.

6.2.4.1. Community-based conservation

Many of the conservation issues identified for *Amazona barabdensis* by this research project are anthropogenic in origin. The long-term success of ecosystem conservation will not be possible without community support and thus community-based conservation is the foundation of CARIB's conservation work. CARIB will work closely with Sea Turtle Conservation Bonaire (STCB) and Salba Nos Lora (Save Our Parrot) to unite parrots, flamingos and turtles as flagship species with which to promote terrestrial, aquatic and marine ecosystem conservation. An important initial research focus for CARIB is to assess community attitudes towards conservation.

6.2.4.2. Habitat protection and restoration

An initial policy objective for CARIB will be to gain protection for important parrot breeding areas, identified by this research project, that are outside the national park.

Subsequent policy work will be to address the feral goat problem. CARIB will be actively involved in restoring diversity and structure to the habitat through projects such as establishing a nursery for native plants and horticultural research. As shown in Chapter III and IV this will probably benefit breeding and non-breeding parrots and also various other birds species.

6.2.4.3. Species management

Initially remaining focused on parrot conservation, our species management will tackle the ecological threats identified by this research project that are not addressed in other CARIB themes. For example, the on going repair of former nest trees and provision of nest boxes in combination with further research into parrot nest site selection, predator control to reduce nest failures and fostering chicks from repeatedly poached nests into other nests. A long-term goal is to reintroduce parrots to Aruba (from where they were extirpated) if assessments show it is ecologically feasible.

6.2.4.4. Capacity building

Extending community education to engage Bonairean children through nature experiences and active involvement with conservation will be the foundation of CARIB's strategic capacity building program. In partnership with Eco-Tourism Bonaire CARIB will provide training for local nature experience guides. CARIB will again work with STCB to build regional conservation capacity in their areas of expertise. Sam Williams is co-chair of the Society for Conservation and Study of Caribbean Birds' (SCSCB) Parrot Working Group. This position provides the opportunity to stimulate communication between regional conservationists and thus improve access to the collective knowledge resource. A future goal for CARIB will be to work with the SCSCB to hold workshops on Bonaire that explore parrot conservation field techniques and bring the network of conservationists together.

6.2.4.5. Monitoring

In order to assess the effectiveness and cost effectiveness of conservation efforts, scientifically robust monitoring will be an ongoing feature of the organizations work.

6.2.5. HOLISTIC ECO-LIVING PROJECT OBJECTIVES

The Holistic Eco-Living Project (HELP) will be an organisation that is actively involved reducing the environmental impact of residents and tourists on Bonaire. HELP will develop and operate projects such as community composting, in order to reduce the quantity of waste entering the landfill. Other projects will involve working with the public to demonstrate simple solutions to ecological problems. For example HELP will facilitate efficient water use, home rainwater collection and grey water recycling.

The most significant and long-term goal for HELP will be to adopt an Eco-Tourism Standard certification scheme and work with the existing tourism industry to achieve a more sustainable industry. The mission of the Holistic Eco-Living Project is:

> *"To provide effective and efficient solutions to mitigate detrimental impacts humans have on the environment, and to educate and encourage others so they may do the same."*

6.2.6. OBJECTIVES SUMMARY

The collective goal of The Quad is to achieve the mission of Conservation Bonaire. Each organisation has its own objectives as outlined above. The following figure summarises these objectives.

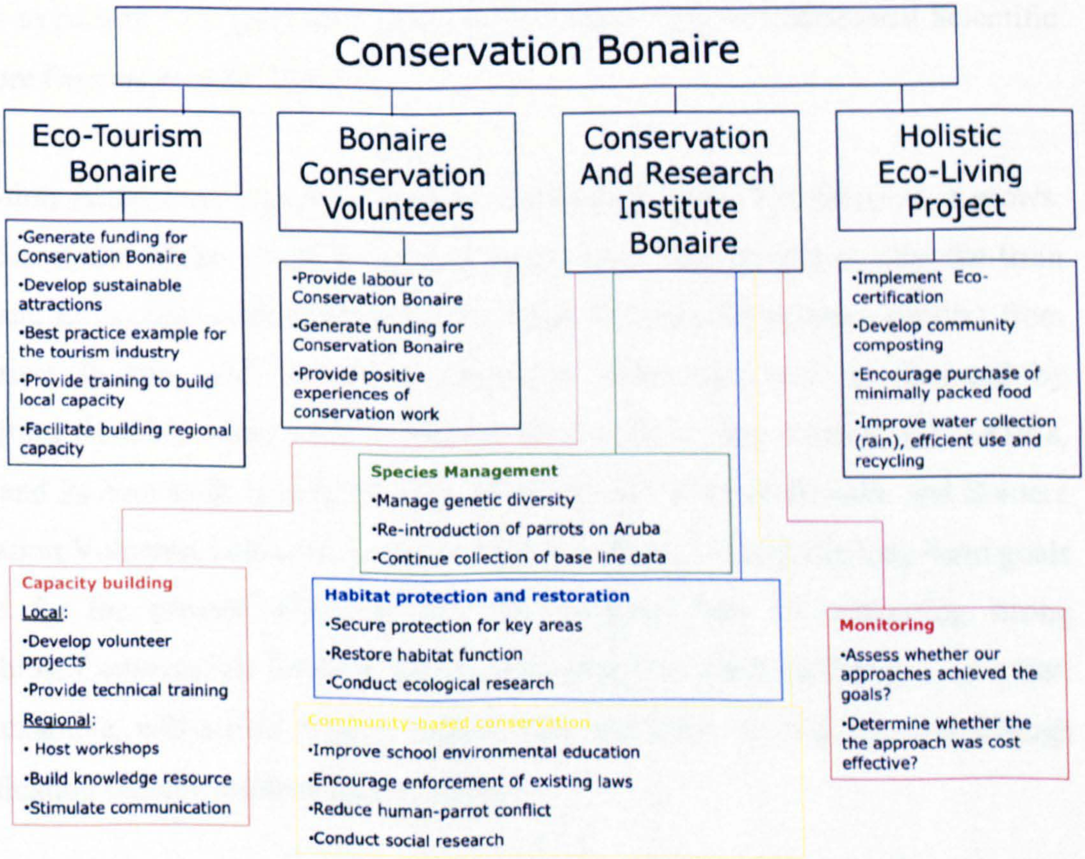

FIGURE 6.3. The objectives of the Quad

6.3. OPERATIONS

6.3.1. CONSERVATION BONAIRE OPERATIONS

Conservation Bonaire will provide direction and administrative services to The Quad that will make economical use of resources so that The Quad personnel can focus on achieving their missions. Conservation Bonaire will operate from offices at the Eco-Lodge and its only physical infrastructure will be computers and office equipment.

It will be essential for Conservation Bonaire to work closely with its partners and establish new relationships in commercial sectors. Through our work with the yellow-shouldered Amazon parrot we have begun the process of establishing ourselves within the community on Bonaire and we have developed outstanding professional relationships. We have met and discussed Conservation Bonaire with: Dutch Caribbean Nature Alliance, STINAPA Bonaire, the National Parks Authority, Sea Turtle Conservation Bonaire, Salba Nos Lora (Save Our Parrot), and Progressive Environmental Solutions. We have also develop a good relationship with Bonaire's Commissioner for the Environment. In all cases, the idea of Conservation Bonaire was very well received. Indeed in September 2009 the Commissioner for the Environment invited us to partner on a grant application to the United Nations Educational Scientific and Culture Organization (UNESCO).

Conservation Bonaire will grow in order to continue to serve The Quad as it grows. Sam Williams and Rhian Evans will lead Conservation Bonaire and in time the team will expand to include administrative staff. Grant income and surplus (profits) from Eco-Tourism Bonaire and Bonaire Conservation Volunteers will be managed by Conservation Bonaire, which will be responsible for paying the salaries of CARIB's, HELP's and its own staff. It will not be possible for Eco-Tourism Bonaire and Bonaire Conservation Volunteers alone to generate sufficient funds to reach the long-term goals we have for the project. However, we are confident that by cultivating strong relationships, Conservation Bonaire, and in particular Eco-Tourism Bonaire, as a best practise example, will attract further support from the wider tourism industry through the certification scheme implemented by HELP.

In order to direct financial support to community projects Conservation Bonaire will establish the Community Projects Allocation Committee. This will be a committee of stakeholders, including Conservation Bonaire personnel, members of the Tourism

Industry and most importantly community leaders. The committee will develop the criteria by which community projects are selected. These criteria will be widely disseminated to encourage the development of further community project applications. We wish to highlight our belief that the involvement of local stakeholders is critical to the success of this process.

6.3.2. ECO-TOURISM BONAIRE OPERATIONS

Eco-Tourism Bonaire will form the physical presence of Conservation Bonaire. The Eco-Lodge will be a low impact development from which all the Conservation Bonaire organisations operate. Eight cabins for Eco-Tourists will be located to provide peace and tranquillity. Staff housing will provide accommodation for staff and long-term visitors, including 'research tourists'. Volunteer tourists will be accommodated in dormitories. Dining and social areas will be designed so as to promote interaction between Eco-Tourists, conservationists and researchers but also to allow Eco-Tourists privacy should they wish.

The Eco-Lodge will be located in a secluded wilderness area within walking distance of key parrot breeding, feeding and roosting areas. The habitat in this area, as with all of Bonaire, has been degraded. Conservation Bonaire will act as stewards and restore the ecology through CARIB's habitat conservation efforts. Locating The Eco-Lodge in an awe inspiring location and creating a positive energised atmosphere will greatly enhance the attraction for all visitors and aid our recruitment of all volunteers. The Eco-lodge will provide a hub of offices for the organisations as well as storage and parking facilities. Eco-Tourism Bonaire will have vehicles for its operations. Vehicles from a rental company will be available for Eco-tourists but we will encourage the use of local taxis where possible.

Eco-Tourism Bonaire will work with CARIB and its partners, namely Sea Turtle Conservation Bonaire to develop guided, sustainable nature experience activities. Having charismatic flagship species such as parrots, flamingos and turtles, central to Conservation Bonaire will make Eco-Tourism Bonaire attractive to our markets. Activities will include observation hides that allow close viewing of feeding parrots, field trips with conservationists or researchers to monitor parrot nests, guided snorkelling or diving at turtle hot spots, observation hides at the flamingo breeding sanctuary. Additionally we will explore the potential for developing other activities such as guided tours of cultural or geographical interest. Rather than employing staff to guide tourists on these activities, Eco-Tourism Bonaire will set the stage, provide training and facilitate local enterprises wishing to take advantage of this opportunity.

The newly developed activities will be available to residents on Bonaire at discounted rates, and other tourists, perhaps at higher rates. In particular this will allow Eco-Tourism Bonaire to attract divers, the majority of whom are nature enthusiasts. Divers must not dive on the day prior to air travel and so represent a large potential market. Products associated with the experience will be available to the visitors for sale or rent. These may include items that are useful for the activity such as packed food and drinks, a snorkel and mask, through to binocular rental; products to take home that remind the individual of the experience, such as T-shirts, key rings or even a glossy coffee table book; or additional material for further learning following the activity.

Eco-Tourism Bonaire will be run by a manager who will be responsible for the lodge and for co-ordinating Eco-Tourist's activities with the local guides. Trainees from the island's catering and hospitality schools will staff The Eco-Lodge. To support local and regional capacity building Eco-Tourism Bonaire will provide a facility for Conservation Bonaire and it's partners to host workshops.

Eco-Tourism Bonaire will initially be marketed heavily through lifestyle, tourism and bird enthusiast magazine articles and advertising. Sam Williams recently secured an eight page article on the Bonaire Parrot Project, which appears in the July 2009 Audubon Magazine (a US equivalent to the RSPB with over 1.5 Million readers). He has also promoted the project globally in other enthusiast magazines, in British daily newspapers and on the BBC World Service. Eco-Tourism Bonaire is well positioned with a network of established writers and photographers who have pledged to aid this initial (financially free) marketing. It will be essential to conduct considerable market research to ensure optimal marketing in the long-term.

Eco-Tourism Bonaire will grow and develop over several years in order to achieve the vision presented here. In the development of the business plan we will look at the strategy with which we reach this vision. Working with the local community to stimulate enterprise, and the development of nature viewing sites are likely to be the first steps on the ground. Construction at the Eco-Lodge site will progress strategically to serve the needs of Conservation Bonaire as it grows and accommodate staff, researchers, Conservation Volunteers and Eco-Tourist as we have the capacity to manage them.

The start up of Eco-Tourism Bonaire will depend on securing grants and we are working with domestic and international conservation organisations to secure this funding, The World Parrot Trust (WPT) and the Society for the Conservation and Study of Caribbean Birds (SCSCB). As a non-profit social enterprise, with a strong conservation focus, and considerable on island support we are confident we can secure such grants. In the long term Eco-Tourism Bonaire will become self-sustaining and provide support for Conservation Bonaire.

6.3.3. BONAIRE CONSERVATION VOLUNTEERS OPERATIONS

Bonaire Conservation Volunteers will operate from the Eco-Lodge. Volunteers will play an important role in the strategic development of the Conservation Bonaire. Initially The Eco-Lodge where volunteers will stay will be more of a camp. The favourable climate means a simple but comfortable camp can be constructed with little more than roofing and secure storage. The Eco-Lodge will have composting toilets, grey water recycling and an off the grid water supply (by truck), which is common on the island. The location of the Eco-Lodge will minimise the need for daily transportation as initially volunteers will be involved in developing infrastructure at The Eco-Lodge and in the surround area (e.g. building interpretive walking trails). Similarly later projects such as ecological fieldwork with CARIB (e.g. habitat restoration or parrot monitoring) will be conducted on foot from the lodge. Bonaire Conservation Volunteers will have a vehicle and trailer with which to transport volunteers and their belongings. The only other physical infrastructure will be their tools.

Sam Williams and Rhian Evans will manage the development of Bonaire Conservation Volunteers and will run the initial work programs with the voluntary help of an experienced volunteer manager. A program manager will be recruited once the business has sufficiently regular work trips. This position may be part time, in which case the individual will have other part time responsibilities within Conservation Bonaire. CARIB, HELP and STCB (turtles) will be involved in setting up relevant work programs but these will be managed to ensure minimal drain on the resources of those organisations for the maximum labour benefit. All programs will be developed to provide rewarding experiences for the participants.

The marketing and cost of different work programs will be targeted and priced according to the theme of that programme. We will build a network of marketing contacts such as university sport clubs and biology departments to initially attract potential volunteers. We will also encourage volunteers to promote their activities upon returning home. This marketing will also benefit Eco-Tourism Bonaire. A dedicated and feature rich website to be our main way of interacting with prospective volunteers. A very attractive element of the Conservation Bonaire structure is that by eliminating a recruitment agency, which may take up to 50% of the volunteers fee, we will be able to charge less and yet still function as a genuine "eco" business that is directly connected to, and funding, community and conservation projects.

Bonaire Conservation Volunteers could run work programs within a year. Initially the business will run from a camp as described, but as the project grows, the accommodation will be refined. The Eco-Lodge will provide the board and lodgings and Bonaire Conservation Volunteers will pay for these services. Individually the Conservation Volunteers may also buy products and refreshments from the Eco-Lodge shop. Bonaire Conservation Volunteers will be a non-profit business and its surplus (profits) will be directed back into Conservation Bonaire.

6.3.4. CONSERVATION AND RESEARCH INSTITUTE BONAIRE (CARIB) OPERATIONS

CARIB will be a collection of resident and visiting conservationists and scientists. These individuals will collectively work towards achieving the various objectives of CARIB. Continuation of the long-term parrot monitoring will form the core of CARIB's work. The direction of this research will be guided initially by the findings from this PhD and that of Rowan Martin. In addition to ecological fieldwork CARIB will fully enter new areas of conservation. Traditionally in conservation, such a goal would be tackled by biologists but CARIB will recruit a team which includes educators, policy advisors and community developers as well as biologists. CARIB personnel will work closely with other NGOs, for example locally with STCB on raising community conservation awareness; or regionally with the SCSCB to work towards better legislation for environmental protection. In each case these partnerships will enable both organisations to achieve their goals through making the best use of the available resources. Building regional capacity in bird and turtle conservation is a goal of CARIB and SCSCB, and, STCB and Wider Caribbean Sea Turtle Conservation Network (WIDECAST). CARIB through its association with The Eco-Lodge would be able to host workshops with local and regional partners in order to achieve this goal.

Eco-Tourism Bonaire will provide CARIB with accommodation, office facilities and storage. CARIB's physical infrastructure will range from vehicles, office equipment (including computers), research equipment and tools. Through its association with Eco-Tourism Bonaire and the Eco-Lodge, CARIB will be in an excellent position to attract long-term volunteer staff. Similarly CARIB will be an attractive partner for research collaborations, because of the organisation's structure and the pro-active research environment we will foster. CARIB will broaden its research focus through attracting such collaborations.

CARIB will minimise running costs through recruiting seasonal or longer-term volunteers who are provided board and lodgings in return for their services. Building strong research collaborations will generate research tourism and form a source of income for The Eco-Lodge. CARIB personnel will also provide services to Eco-Tourism Bonaire by interacting with guests and giving evening presentations. This interaction enhances the product of Eco-Tourism Bonaire but also benefits visiting researchers who are increasingly expected to have the skill to communicate their research to the public. Ultimately CARIB will be supported through Eco-Tourism Bonaire and domestic funding from other sustainable tourism revenue. None the less CARIB will be dependent on grants to operate in the first years and for it to develop. We are working with domestic and international conservation organisations to secure funding.

6.3.5. HOLISTIC ECO-LIVING PROJECT (HELP) OPERATIONS

HELP will work at all levels to mitigate environmental problems. HELP personnel will use science to inform policy, and work with politicians to raise awareness of environmental sustainability issues. They will work with businesses to reduce the impact of their customers. Working directly with the customers and local communities HELP will work with CARIB in using strategic social marketing to raise awareness of issues, which the public can influence. Help will target key environmental issues that affect Bonaire and provide simple and low cost solutions.

HELP will primarily function as a consultancy that uses working examples of solutions at The Eco-Lodge. A likely exception, where HELP will be directly involved in the execution of a project will be in the development of a community composting scheme. The key project for HELP will be to implement an eco-tourism certification scheme. To do this it will be necessary to find a way to engage established businesses, for which achieving the first level of certification will likely require more investment that they are prepared to make. HELP will work with an existing and credible scheme to develop a series of smaller steps that recognise and reward businesses that show progressive environmental attitudes and attempt to minimise their impact. Naturally, HELP will be able to provide expertise and assist businesses in becoming more sustainable. By simultaneously educating dive tourists we hope that businesses will become competitively eco friendly to attract this market. Thus HELP will provide a good reason for businesses to reduce their impact and an avenue through which they can support conservation and the local community.

HELP will operate from the Eco-Lodge and the HELP staff will be accommodated at the lodge. The organisation will need only limited office facilities including a computer. Other infrastructure will include a vehicle and tools. As with CARIB long-term volunteers will form the majority of HELP's staff. It will be necessary to employ a professional environmental consultant with relevant expertise to lead the projects. HELP personnel will provide services to Eco-Tourism Bonaire by interacting with guests and giving evening presentations. They may also consult directly with Eco-Tourists to discuss how they might reduce their environmental impact at home. HELP will also create a market for various eco products (ecological soap through to solar cookers) that could be sold in the Eco-Lodge shop. It may also be possible to stimulate local enterprise to take advantage of this market.

The scale of HELP and the projects it tackles will depend on the level of funding secured. Initially HELP will depend on grants but over time the organisation will be supported through Eco-Tourism Bonaire and domestic funding from other sustainable tourism revenue.

6.3.6 OPERATIONS SUMMARY

The collective goal of The Quad is to achieve the mission of Conservation Bonaire. Each organisation has a distinct role, yet they all benefit from the exchange of services between one another beneath the Conservation Bonaire umbrella. The relationship between Conservation Bonaire, The Quad, The tourism industry, and the Community Projects Allocation Committee is shown in Figure 6.4.

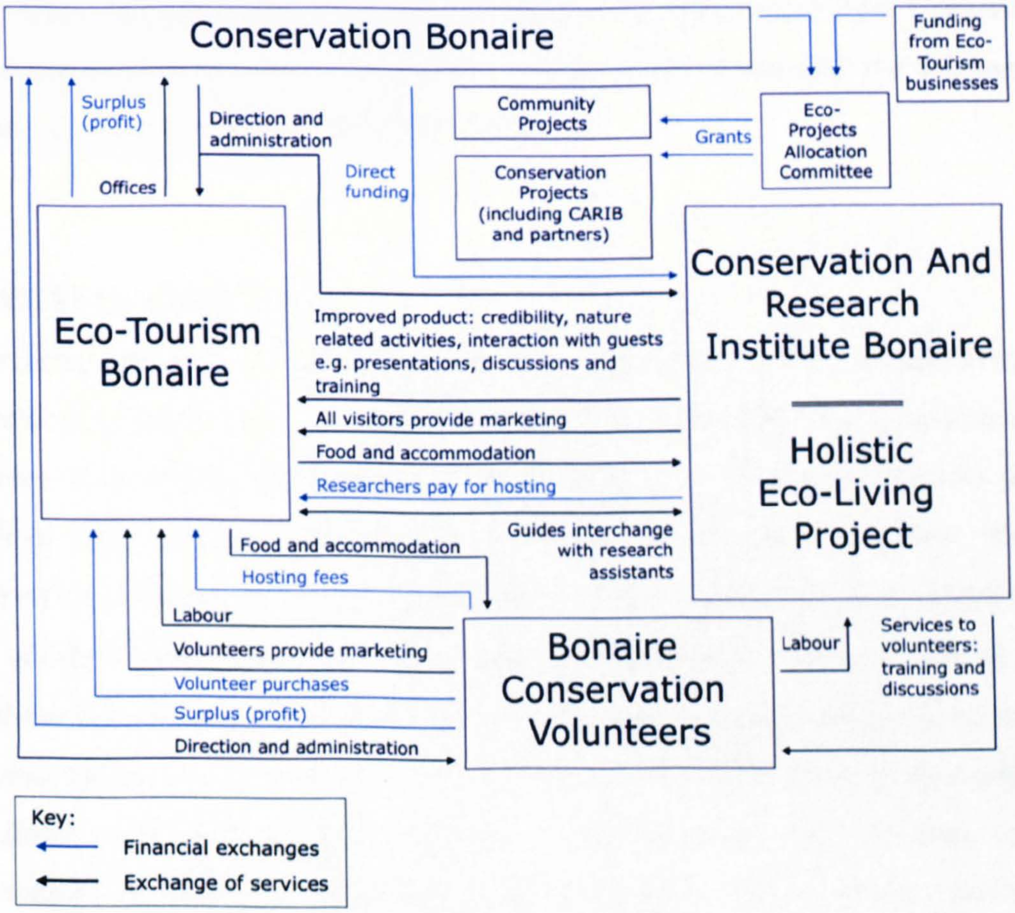

FIGURE 6.4. The Conservation Bonaire Model, showing financial, operational and marketing relationships. CARIB and HELP only occupy the same box here for simplicity; they function as separate organisations with their own exchanges.

6.4. BUSINESS MODEL

Conservation Bonaire as outlined here is an evolution of the successful model developed between an independent volunteer recruiting organisation, an eco-tourism lodge, and a research project located in a remote rainforest area called Tambopata, in Peru. There are a number of critical additions in the Conservation Bonaire model.

Firstly rather than use an independent volunteer recruiting organisation which may take over 50% of the fees volunteers pay, Bonaire Conservation Volunteers will play this role resulting in considerably more funding coming into Conservation Bonaire.

A further and significant addition to the model is HELP, because of its role in mitigating the environmental impact of residents and tourists, but more importantly because it presents the opportunity for the existing tourism industry to become more sustainable. The involvement of the existing tourism industry in this model is what sets Conservation Bonaire apart from other conservation approaches. The Conservation Bonaire model also provides a framework, which serves to structure the relationships between Conservation Bonaire and its partners.

6.5. OVERALL SUMMARY

Conservation Bonaire will bring together key components of the conservation and environmental movements to achieve sustainable development for the benefit of the Bonairean community. Eco-Tourism Bonaire will be a sustainable tourism project providing exclusive accommodation and intimate encounters with nature. Bonaire Conservation Volunteers will provide labour for Conservation Bonaire organisations while giving volunteers positive and memorable experiences of conservation work. Both these non-profit tourism businesses will financially benefit the local community and conservation. The Conservation And Research Institute Bonaire will be a collection of resident and visiting conservationists and scientists that develop creative conservation approaches, including capacity building, and conduct outstanding scientific research. The Holistic Eco-Living Project will provide solutions to mitigate detrimental impacts of residents and tourists on the environment.

These organisations will operate from The Eco-lodge, which will be a collection of low-impact offices, accommodations and storage buildings. When established the Conservation Bonaire model will serve as a conservation approach of regional and possibly global significance. Conservation Bonaire will enable the island on Bonaire to achieve sustainable economic growth and to promote itself as "The Eco-island of the Caribbean".

Chapter VII

DISCUSSION

7.1 OVERVIEW

Biotic and abiotic factors can limit populations by influencing the life history, abundance and distribution of individuals (Norris, 1993; Martin, 1995; Newton, 1998; Verhulst & Nilsson, 2008). Understanding the patterns, mechanisms and consequences of these relationships is central to ecology and fundamental for conservation. The overarching goal of this study was to identify key factors that influence the yellow-shouldered Amazon parrot (*Amazona barbadensis*) on Bonaire and by doing so provide information that could benefit the future conservation of this and other species. This was achieved through analyzing patterns in life history traits, nest success and reproductive success, the factors affecting productivity, the factors affecting spatial and temporal distribution and nest site selection and limitation, as presented in Chapters II – V. This information will benefit future conservation efforts for *A. barbadensis* on Bonaire and has led to a much broader conservation proposal, which I hope to develop and implement (Chapter VI).

7.2. SUMMARY OF CHAPTERS

Understanding the Bonaire *A. barbadensis* population's life history, nest success and reproductive rates was an essential starting point for this study (Chapter II). These measures have been described for other *A. barbadensis* populations and indeed other *Amazona* species, however examining the situation specifically on Bonaire proved worthwhile and interesting. Reproductive rates were generally lower on Bonaire than those reported for the Margarita population (Sanz & Rodríguez-Ferraro, 2006). Nest success and productivity were typical for the genus experiencing contemporary conditions. However as "contemporary conditions" include a suite of anthropogenic limits, with all but one of the studies on *Amazona* species in Table 2.4. reporting chick losses due to poaching, these rates are almost certainly lower than could be achieved under historical "natural" conditions. Hatchability was low for *A. barbadensis* and two other *Amazona* species. Each of these three populations has experienced a population bottleneck and the low hatchability probably results from inbreeding depression (Briskie & Mackintosh, 2004).

A natural progression for this study was to then investigate how the Bonaire *A. barbadensis* population's reproductive biology was affected by an array of potential limiting factors. Thus, in Chapter III I examined how productivity (clutch size, brood size and chick asymptotic weight) were related to: timing of breeding, proximity to food resource patches and neighbours, habitat quality, competitor abundance, predator presence, and nest structural characteristics. Each of the three productivity measures was influenced by different factors. Clutch size increased when the food resource (on two scales) was greater. Brood size prior to fledging was greater where there were fewer pigeons and parakeets and where predators were absent. Chick asymptotic weight was greater in less exposed nests. While the mechanisms through which these factors influence productivity are uncertain it would not be difficult to develop management strategies based on these results to boost productivity.

In addition to influencing a species' reproductive biology, limiting factors will also influence the abundance and distribution of a population, both spatially and temporally (Andrewartha, 1954; Fretwell & Lucas, 1969; Holmes et al., 1979). I investigated how the spatial abundance of *A. barbadensis* was influenced by habitat structure and competitor abundance in Chapter IV. *A. barbadensis* was found in greater abundance in areas of more mature vegetation, i.e. greater tree coverage, more tall and large trees. This finding highlights the importance of natural areas with mature habitat for the *A. barbadensis* population and lends support to concern over habitat loss. In Chapter IV I also investigated the seasonal movements of *A. barbadensis* and found that these were correlated with the previous month's rainfall. Rural roosts were occupied following rainy months (approximately September to February), whereas following dry months (approximately March to August) urban roosts became occupied and rural roosts were unoccupied. It is likely that the irrigated gardens and public urban areas provide better foraging than the degraded rural habitat during dry periods. This migration does, however, raise two important conservation concerns. The loss of cultivated fruit creates a parrot-human conflict, and several parrots are killed in collisions with traffic. It is possible that mortality may be even greater if *A. barbadensis* remained in the rural areas during dry periods. Consequently anthropogenic change may have actually benefited the parrots, or at least mitigated the negative impact of habitat degradation.

Cavity nesting species, and in particular secondary cavity nesters are often limited by the availability of cavities (Brawn & Balda, 1988; East & Perrins, 1988; Gustafsson, 1988; Garcia-Navas et al., 2008). To examine whether this was case on Bonaire in Chapter V I described nest sites used by *A. barbadensis*. Using this information I then searched for available cavities to assess whether there were apparently suitable cavities that were unused. I also compared the characteristics of used and unused cavities to determine resource selection functions to identify the most important characteristics. Finally, I experimentally increased the availability of nest sites to test whether the population was nest site limited. *A. barbadensis* on Bonaire used nest cavities with a wide range of characteristics. This may indicate nest sites are limited or it could suggest *A. barbadensis* is a generalist with regard to site characteristics. Apparently suitable, but unused cavities were found and these were particularly abundant in one habitat type. The resource selection function indicated that four characteristics were important in nest site selection. Two of these characteristics: entrance diameter and nest entrance size, were consistent with nest site preference in other cavity-nesting bird species. Three of the ten repaired former nest sites were reused immediately but none of the 12 nest boxes provided were used. Why the apparently suitable tree cavities and the nest boxes were unused is uncertain, but the combination of these results and the general difficultly of getting many parrot species to use boxes, highlights gaps in our knowledge of parrot nest site preferences.

Drawing on my belief that conservation biology must be followed by action to realize its full value, and my goals to set up a long-term conservation project on Bonaire, Chapter VI provides a business proposal for a multifaceted enterprise I am developing. A modified version of this proposal recently won a business plan competition at the University of Sheffield. Through partnerships with several organizations, I hope to provide a new economic model for Bonaire that will enable the development of sustainable tourism that promotes the conservation of wilderness areas and supports the local community. I hope to provide management for key conservation issues that have been identified through this, and my research colleague Rowan Martin's, work, and by developing research collaborations I also hope to facilitate further scientific research that may benefit conservation management and inform policy.

Overall this study has added to our knowledge of parrot biology first by providing a description of the Bonaire population's reproductive biology and by identifying interesting areas for future conservation and research interest. This work has also illustrated how parrot productivity is influenced by specific biotic and abiotic factors, all of which could be managed to benefit conservation in the future. Describing the spatial and temporal distribution of parrots on Bonaire has provided new insights to parrot habitat requirements. Finally this study has added to our knowledge of parrot nest site selection and identified key areas requiring further study.

7.3. IMPLICATIONS OF FINDINGS AND FURTHER STUDY

A. barbadensis is considered vulnerable to the threat of extinction by the IUCN (2008) so it is a worthwhile target for conservation concern. The rates of nest success and productivity observed for the *A. barbadensis* population on Bonaire are typical of those reported for *Amazona* species (Chapter II). Rather than indicate that the Bonaire population experiences typical rates for an *Amazona* species under natural conditions, it is more likely that these findings indicate the dire situation for many *Amazona* parrot species. The notably higher reproductive rates observed for Hispanolian Amazon parrots (*A. ventralis*) give and indication of what all *Amazona* populations might achieve in the absences of anthropogenic disturbance (Snyder et al., 1987).

Several conservation projects have demonstrated that rates of nest success and productivity can be increased through management to alleviate threats to parrot populations. Unfortunately increasing recruitment and adult survival rates are typically more elusive targets. On Bonaire as with the Puerto Rican parrot it seems the low proportion of breeding birds is also a concern (Beissinger et al., 2008). As this clearly has implications for recruitment it must be a priority for future study. Rapid population recovery, however it is achieved, may be a critically important goal for species conservation because of the potential long-term consequences of low population size. There is some evidence that long population bottlenecks may effectively purge small populations of deleterious mutations and allow apparently healthy population recovery, as with the Mauritius kestrel (*Falco punctatus*) and Chatham island black robin (*Petroica traversi*), (Temple, 1986; Ardern & Lambert, 1997). However, Jamieson et al. (2006) argued that complete purging is unlikely and that conservation management must still aim to maximize genetic diversity.

Historically, *A. barbadensis* has experienced population bottlenecks during droughts (Voous, 1983). It is likely these events have resulted in inbreeding depression and possibly the poor hatchability observed in this study. This situation highlights the value of working with a vulnerable species like *A. barbadensis*. The Bonaire population presents the interesting opportunity to explore the patterns of low hatchability of pairs through a combination of genetic research and hands on management techniques. The latter may include the removal of inbred individuals or pairs from the breeding population, which would be inappropriate for more endangered species. Furthermore, investigating the development of embryos in unhatched eggs provides an additional route to understanding the cause of hatching failure. Using a wild population of *A. barbadensis* to explore the basis for low productivity could benefit the conservation management of other more endangered species.

This study has shown that on Bonaire, measures of productivity and spatial distribution are influenced by various habitat and community factors. At a fine scale, greater food resources near the nest increased clutch size, whereas at a larger, island-wide scale, areas of more mature habitat had greater abundance of *A. barbadensis*. It is well known that food can constrain survival and reproduction during breeding and non-breeding seasons and that the mechanisms by which such constraints impacts on individuals can be complex (Cody, 1974; Kenward & Sibly, 1977; Holmes et al., 1979; Martin, 1987; Newton, 1998). This study adds to that body of literature and provides new insights relevant to long-lived species and island populations. From a scientific perspective it would be interesting to work out the mechanisms driving the observed patterns of clutch size. Examining whether the particular tree species that correlate with clutch size are important because those species enable females to reach good condition could be tackled by conducting replicated food supplementation experiments including control pairs with no or nutritionally different foods. It would also be necessary to examine the fruit tree's phenology because those species may simply be important because they produce food at a critical time.

Determining whether the observed spatial distribution is driven by *A. barbadensis*' preference for more mature vegetation for protection from predators or the elements, or whether these areas provide more food would also be interesting. While the mechanism driving the pattern of distribution may differ from that driving clutch size it is likely that they both ultimately result from habitat degradation. Likewise, the temporal patterns of

A. barbadensis distribution may ultimately be the result of human activity if the loss of plant diversity has reduced the food resources available to *A. barbadensis* during dry periods. The impact humans have had on the terrestrial ecosystems, and continued degradation by goats is dramatic (De Freitas, 2005). From a conservation perspective the direction of future efforts in this area are very different to the direction of research. In the short-term a priority for management would simply be to initiate goat eradication and habitat restoration. Empirical research to monitor the effectiveness of such efforts and to assess the bird community's response would be a fascinating addition that could help guide long-term efforts. By contrast pure research project might take advantage of the outstanding opportunity Bonaire offers for a large-scale habitat restoration study. This could involve replicated exclusion, control and even enclosure plots with different combinations of goats, rats and cats present or absent. In addition this design might also include different flora restoration techniques such as provision of compost or other growing medium and/or irrigation. A robust experimental study of this nature might help avoid ecological disasters resulting from conservation management, such as the recently reported rabbit population explosion on Macquarie Island following the eradication of introduced cats (Dana et al., 2009; John et al., 2009).

A. barbadensis productivity and distribution were also associated with the distribution and abundance of other members of the bird community. This study did not investigate the precise relationships between species and it is not possible to conclude the extent to which competition occurs or the mechanism by which it impacts *A. barbadensis*. Unlike the situation with habitat, it would be inappropriate to attempt to manage "competitor" species without further study of the observed patterns. This would require a higher resolution study, possibly with the removal specific species. Such a study of community level processes, particularly in response to the proposed habitat restoration, could be very interesting and valuable for island ecosystem conservation.

The dramatic negative effect of rats and cats on island bird populations is well known (Robinet et al., 1998; Jones, 2005; Igual et al., 2007; BirdLife, 2008a). The techniques for predator removal (poisoning), as pioneered by New Zealand conservationists, are also now well established (Jansen, 2005; Moore, 2005; Tatayah et al., 2007) and a nest site specific approach may be considered for future conservation management on Bonaire. This is likely to benefit several other bird species and may be justified for community ecology conservation. However, the impact of rat poison on reptile communities poorly understood (Glen et al., 2007; K. Swinnerton pers. comm.). Fortunately Bonaire provides an excellent opportunity to study this, in addition to developing poison stations in plots around parrot nests it would be possible to have un-baited control nest plots, random plots with poison stations, and random control plots. This interesting study would provide valuable insight into the impact of poisoning techniques on reptile communities and would thus provide further justification for the management strategy. Determining whether predator removal represents a cost effective conservation approach for a long-lived parrot would require evaluation of the short-term benefit to population growth and the long-term benefit in terms of maximizing genetic diversity. Preventing complete nest failures through predator control is likely to contribute to the latter. Increasing survival at later life stages may be more cost-effective for population growth, however, there may be no substitute for managing the genetic diversity currently available in the population.

Nest site characteristics were shown to influence chick asymptotic weight with chicks reaching greater weights in less exposed nests. The long-term fitness consequences of offspring condition are unknown in parrots but are likely to be similar to other species (Dijkstra et al., 1990; Stearns, 1992). Increasing numbers is likely to be the principal objective in any species conservation, particularly for critically endangered species, but management strategies for long-lived species may also benefit from the production of high quality offspring.

As was to be expected, this study generated as many questions as it answered and further research on nest site availability and the proportion of breeding birds in the population in particular, would be worthwhile. Apparently suitable natural cavities were available in the environment, and nest boxes that matched dimensions used by parrots were provided, yet these were unused despite apparent competition for nests (R. Martin pers. comm., pers. obs.). The resource selection function identified specific nest characteristics that were important for cavity selection but there remain numerous gaps in our knowledge of parrot nest site preference. Although productivity (as measured) was not influenced by nest site clustering, it is not possible to rule our social preferences for *A. barbadensis* nest site suitability. Furthermore habitat factors external to the nest cavity may also be important for nest site selection. Food resource at the nest for example was found to correlate with clutch size and may be important in site selection.

Possibly the most concerning finding that the various elements of this research collectively indentify is the remarkably low number of breeding birds in the *A. barbadensis* population on Bonaire. Similar estimates can be generated from the likely number of breeding birds (21.5%; Chapter II), and when considering apparently non-breeding birds counted in urban areas (e.g. July 2008, 540 non breeders from a population of 650 = 110 breeders or 17%; Chapter V). This large proportion of non-breeders may result from nest site limitation but it may just be a typical feature of long-lived parrot populations. Large numbers of non-breeding birds have been seen in other parrot species and it is unknown what proportion of any parrot population may breed (Snyder et al., 1987; Beissinger & Bucher, 1992a; Beissinger & Bucher, 1992b; Munn, 1992; Kyle, 2005).

On Bonaire the age structure of the population is unknown and estimating the number of potential breeders is further complicated by the apparent population increase since 2002 (Low, 2005; Forshaw, 2006). However, it is likely that even before 2002 there were more than 110-140 sexually mature individuals. Constructing models with various age structures to examine which most closely follows the observed population dynamics on Bonaire in combination with ongoing ringing and re-sighting efforts will hopefully provide some clarity on this matter and may also aid the assessment of nest site limitation. Finding a way to increase the number of breeding birds, if indeed possible, is clearly an important goal for population growth or, in some cases, recovery. Unfortunately however, our current lack of knowledge on parrot nest site selection reduces our ability to effectively test whether parrot populations are nest site limited and as such also hinders our ability to conserve threatened parrots.

7.4. FINAL THOUGHTS AND THE FUTURE

With so much still unknown about parrots and so much to do to protect them it seems almost impossible to know where to begin. In light of this is seems fair to ask: How does this work help parrots? I'd like to believe that this research will benefit parrots because it identifies how specific aspects of the habitat influence productivity and distribution. It also furthers our knowledge on parrot biology, and highlights interesting areas for further study, in particular hatchability, competition and nest site preferences. This, I hope, will stimulate further research in these areas and refine our understanding of the patterns observed on Bonaire. If further research can take place in combination with conservation efforts so much the better. The findings from this study do have a specific place within the lofty ambitions for future conservation and research, and it is fantastic to be able to end this project with a vision for the future that I believe will benefit parrot conservation on Bonaire.

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APPENDICES

Appendix 1. Models and parameters from the 95% confidence set for analysis a: clutch size ~ initiation date (Idate) + proximity to food resource patch (P-food) + proximity to the second neighbour (P-2nd neigh) + number of nests within 200m (Nests in 200m), (n = 40). The table indicates the parameters included in the model, the number of parameters (*K*), the AICc, delta weight (Δ_i ; difference between the AICc of the given model and the AICc best) and the model selection probability (w_i). The latter we recalculated to sum to 1 within the confidence set. Parameter estimates (ß) were calculated by summing across the models within the confidence set (weighted by the confidence set model selection probability).

	Idate	**P-food**	**P-2nd neigh**	**Nests in 200m**	***K***	**AICc**	Δ_i	w_i
AICc best		I			1	115.151	0	0.256
		I	I		2	115.739	0.588	0.191
	I	I			2	117.063	1.912	0.098
	I				1	117.462	2.311	0.081
		I		I	2	117.588	2.437	0.076
	I	I	I		3	117.957	2.806	0.063
		I	I	I	3	118.055	2.903	0.060
			I		1	118.465	3.314	0.049
				I	1	118.816	3.665	0.041
	I		I		2	119.252	4.100	0.033
	I	I		I	3	119.665	4.514	0.027
	I			I	2	119.756	4.605	0.026
Selection probability	0.327	0.771	0.396	0.229				
ß	-0.049	-0.247	-0.079	0.003				

Appendix 2. Models and parameters from the 95% confidence set for analysis b: clutch size ~ habitat principal components 1 + 2 + 3 + 4 + 5, (n = 30). The table indicates the parameters included in the model, the number of parameters (*K*), the AICc, delta weight (Δ_i ; difference between the AICc of the given model and the AICc best) and the model selection probability (w_i). The latter we recalculated to sum to 1 within the confidence set. Parameter estimates (ß) were calculated by summing across the models within the confidence set (weighted by the confidence set model selection probability).

	PCA1-habitat	**PCA2-habitat**	**PCA3-habitat**	**PCA4-habitat**	**PCA5-habitat**	***K***	**AICc**	Δ_i	w_i
AICc best				I	I	2	79.343	0.000	0.222
		I		I	I	3	79.686	0.343	0.187
			I	I	I	3	80.467	1.124	0.127
		I	I	I	I	4	80.964	1.621	0.099
	I			I	I	3	81.745	2.402	0.067
	I	I		I	I	4	81.756	2.413	0.067
		I	I	I		3	82.910	3.567	0.037
	I		I	I	I	4	83.085	3.742	0.034
	I	I		I		2	83.216	3.873	0.032
	I	I	I	I	I	5	83.249	3.906	0.032
			I	I		2	83.440	4.097	0.029
				I		1	83.963	4.620	0.022
		I			I	2	85.182	5.839	0.012
	I	I	I	I		4	85.226	5.883	0.012
	I	I		I		3	85.340	5.997	0.011
	I		I	I		3	85.509	6.166	0.010
Selection probability	0.232	0.489	0.379	0.988	0.847				
ß	0.028	0.120	0.080	0.554	0.323				

Appendix 3. Models and parameters from the 95% confidence set for analysis c: clutch size ~ bird community (competitor) principal components 2 + 3 + 5 + predator presence (Pred), (n = 16). The table indicates the parameters included in the model, the number of parameters (*K*), the AICc, delta weight (Δ_i ; difference between the AICc of the given model and the AICc best) and the model selection probability (w_i). The latter we recalculated to sum to 1 within the confidence set. Parameter estimates (ß) were calculated by summing across the models within the confidence set (weighted by the confidence set model selection probability).

	PCA2-competitor	**PCA3-competitor**	**PCA5-competitor**	**Pred**	***K***	**AICc**	Δ_i	w_i
AICc best		I	I	I	2	85.724	0.000	0.205
		I			1	86.416	0.692	0.145
			I	I	1	87.132	1.408	0.101
	I	I	I	I	3	87.579	1.855	0.081
	I		I	I	2	88.351	2.627	0.055
		I	I	I	3	88.449	2.725	0.052
		I	I	I	3	88.600	2.876	0.049
		I			2	88.840	3.116	0.043
	I	I			2	88.882	3.158	0.042
		I			2	89.091	3.367	0.038
			I	I	2	89.631	3.907	0.029
			I	I	2	89.770	4.046	0.027
	I	I	I	I	4	90.631	4.907	0.018
	I				1	90.665	4.941	0.017
	I	I	I	I	4	90.703	4.979	0.017
					1	90.777	5.053	0.016
					1	91.036	5.312	0.014
	I		I	I	3	91.161	5.437	0.014
	I		I	I	3	91.207	5.483	0.013
	I	I			3	91.566	5.842	0.011
		I	I	I	4	91.599	5.876	0.011
Selection probability	0.304	0.737	0.632	0.307				
ß	-0.043	-0.249	0.224	-0.050				

Appendix 4. Models and parameters from the 95% confidence set for analysis d: clutch size ~ nest height above ground (Height) + exposure + entrance area + cavity floor area (Cavity area), (n = 38). The table indicates the parameters included in the model, the number of parameters (*K*), the AICc, delta weight (Δ_i ; difference between the AICc of the given model and the AICc best) and the model selection probability (w_i). The latter we recalcualted to sum to 1 within the confidence set. Parameter estimates (ß) were calculated by summing across the models within the confidence set (weighted by the confidence set model selection probability).

	Height	**Exposure**	**Entrance area**	**Cavity area**	***K***	**AICc**	Δ_i	w_i
AICc best		I			1	107.492	0.000	0.312
		I		I	2	108.590	1.098	0.180
	I	I			2	109.328	1.836	0.125
		I	I		2	109.775	2.283	0.100
		I	I	I	3	110.866	3.374	0.058
				I	1	111.017	3.525	0.054
	I	I		I	3	111.083	3.591	0.052
	I	I	I		3	111.939	4.447	0.034
	I				1	112.083	4.591	0.031
			I	I	2	112.257	4.765	0.029
			I		1	112.540	5.048	0.025
Selection probability	0.242	0.861	0.245	0.373				
ß	0.029	0.311	0.023	0.073				

Appendix 5. Models and parameters from the 95% confidence set for analysis e: brood size ~ initiation date (Idate) + proximity to food resource patch (P-food) + proximity to the second neighbour (P-2nd neigh) + number of nests within 200m (Nests in 200m) + clutch size, (n = 50). The table indicates the parameters included in the model, the number of parameters (*K*), the AICc, delta weight (Δ_i ; difference between the AICc of the given model and the AICc best) and the model selection probability (w_i). The latter we recalculated to sum to 1 within the confidence set. Parameter estimates (ß) were calculated by summing across the models within the confidence set (weighted by the confidence set model selection probability).

	Idate	**P-food**	**P-2nd neigh**	**Nests in 200m**	**Clutch size**	***K***	**Δ_i**	**AICc**	**w_i**
AICc best	I				I	2	0	140.691	0.210
					I	1	0.016	140.7063	0.208
			I		I	2	2.152	142.842	0.072
		I			I	2	2.186	142.876	0.070
	I		I		I	3	2.333	143.024	0.065
				I	I	2	2.362	143.052	0.064
	I			I	I	3	2.391	143.081	0.064
	I	I			I	3	2.473	143.164	0.061
	I					1	4.015	144.706	0.028
		I	I		I	3	4.518	145.208	0.022
			I	I	I	3	4.613	145.3036	0.021
		I		I	I	3	4.636	145.327	0.021
	I		I	I	I	4	4.911	145.601	0.018
	I	I	I		I	4	4.919	145.610	0.018
	I	I		I	I	4	4.979	145.670	0.017
		I				1	5.657	146.348	0.012
	I	I				2	6.006	146.697	0.010
	I			I		2	6.365	147.056	0.009
	I		I			2	6.369	147.060	0.009
Selection probability	0.507	0.232	0.224	0.215	0.932				
ß	-0.091	-0.340	-0.297	-0.089	0.288				

Appendix 6. Models and parameters from the 95% confidence set for analysis f: brood size ~ habitat principal components 2 + 3 + 4 + 5 + clutch size, (n = 32). The table indicates the parameters included in the model, the number of parameters (*K*), the AICc, delta weight (Δ_i ; difference between the AICc of the given model and the AICc best) and the model selection probability (w_i). The latter we recalculated to sum to 1 within the confidence set. Parameter estimates (ß) were calculated by summing across the models within the confidence set (weighted by the confidence set model selection probability).

	PCA2-habitat	**PCA3-habitat**	**PCA4-habitat**	**PCA5-habitat**	**Clutch size**	***K***	**AICc**	Δ_i	w_i
AICc best			I		I	2	90.999	0.000	0.136
		I	I		I	3	91.157	0.157	0.126
		I			I	2	91.584	0.585	0.102
					I	1	91.745	0.745	0.094
		I				1	92.372	1.372	0.069
			I	I	I	3	93.214	2.214	0.045
		I		I		2	93.393	2.394	0.041
				I	I	2	93.431	2.432	0.040
		I		I	I	3	93.518	2.518	0.039
	I		I		I	3	93.841	2.842	0.033
		I	I	I	I	4	93.879	2.879	0.032
	I	I	I		I	4	93.930	2.931	0.031
				I		1	93.993	2.994	0.031
	I				I	2	94.210	3.211	0.027
	I	I			I	3	94.272	3.272	0.027
		I	I			2	94.321	3.321	0.026
	I	I				2	94.638	3.639	0.022
			I	I	I	3	95.457	4.458	0.015
	I	I		I		3	95.973	4.974	0.011
	I		I	I	I	4	96.006	5.006	0.011
			I	I		2	96.027	5.028	0.011
	I			I	I	3	96.134	5.135	0.010
			I			1	96.183	5.184	0.010
Selection probability	0.184	0.526	0.477	0.287	0.769				
ß	0.013	0.151	0.139	0.049	0.304				

Appendix 7. Models and parameters from the 95% confidence set for analysis g: brood size ~ bird community (competitor) principal components 2 + 3 + 5 + predator presence (Pred) + clutch size, (n = 38). The table indicates the parameters included in the model, the number of parameters (*K*), the AICc, delta weight (Δ_i ; difference between the AICc of the given model and the AICc best) and the model selection probability (w_i). The latter we recalculated to sum to 1 within the confidence set. Parameter estimates (ß) were calculated by summing across the models within the confidence set (weighted by the confidence set model selection probability).

	PCA2-competitor	**PCA3-competitor**	**PCA5-competitor**	**Pred**	**Clutch size**	***K***	**AICc**	Δ_i	w_i
AICc best		I				1	90.899	0.000	0.147
		I	I	I		2	90.955	0.055	0.143
		I	I	I	I	3	91.413	0.514	0.113
					I	1	91.811	0.911	0.093
		I	I	I		2	92.299	1.400	0.073
			I	I	I	2	92.781	1.882	0.057
	I	I				2	93.048	2.148	0.050
		I				2	93.544	2.645	0.039
	I	I			I	3	93.576	2.677	0.038
		I			I	3	93.745	2.846	0.035
	I	I	I	I	I	4	93.916	3.017	0.032
	I	I	I	I		3	94.270	3.371	0.027
					I	2	94.362	3.463	0.026
	I				I	2	94.434	3.535	0.025
		I	I	I	I	4	94.471	3.572	0.025
		I	I	I		3	95.181	4.281	0.017
	I		I	I	I	3	95.500	4.600	0.015
			I	I	I	3	95.568	4.669	0.014
	I	I				3	95.925	5.026	0.012
			I	I		1	96.303	5.404	0.010
	I					1	96.541	5.641	0.009
Selection probability	0.181	0.915	0.714	0.846	0.572				
ß	0.007	-0.400	-0.250	-0.355	0.160				

Appendix 8. Models and parameters from the 95% confidence set for analysis h: brood size ~ nest height above ground (Height) + entrance exposure + entrance area + cavity floor area (Cavity area) + total number of eggs laid, (n = 48). The table indicates the parameters included in the model, the number of parameters (*K*), the AICc, delta weight (Δ_i ; difference between the AICc of the given model and the AICc best) and the model selection probability (w_i). The latter we recalcualted to sum to 1 within the confidence set. Parameter estimates (ß) were calculated by summing across the models within the confidence set (weighted by the confidence set model selection probability).

	Height	**Exposure**	**Entrance area**	**Cavity area**	**Clutch size**	***K***	**AICc**	Δ_i	w_i
AICc best			I		I	2	134.096	0.000	0.157
			I	I	I	3	134.107	0.012	0.156
				I	I	2	134.799	0.704	0.111
					I	1	135.455	1.359	0.080
	I			I	I	3	136.253	2.157	0.053
		I	I	I	I	4	136.346	2.251	0.051
		I		I	I	3	136.412	2.317	0.049
	I		I		I	3	136.432	2.337	0.049
	I		I	I	I	4	136.486	2.390	0.048
		I	I		I	3	136.564	2.468	0.046
				I		1	137.044	2.949	0.036
			I	I		2	137.591	3.495	0.027
		I			I	2	137.611	3.515	0.027
	I				I	2	137.837	3.742	0.024
	I	I		I	I	4	138.216	4.120	0.020
	I			I		2	138.747	4.652	0.015
	I	I	I		I	4	138.901	4.806	0.014
	I	I	I		I	4	138.984	4.888	0.014
		I		I		2	139.268	5.173	0.012
			I			1	139.566	5.470	0.010
Selection probability	0.237	0.233	0.572	0.579	0.899				
ß	-0.012	-0.018	-0.138	0.148	0.311				

Appendix 9. Models and parameters from the 95% confidence set for analysis i: asymptotic mass ~ initiation date (Idate) + proximity to food resource patch (P-food) + proximity to the second neighbour (P-2nd neigh) + brood size, (n = 24). The table indicates the parameters included in the model, the number of parameters (*K*), the AICc, delta weight (Δ_i ; difference between the AICc of the given model and the AICc best) and the model selection probability (w_i). The latter we recalcualted to sum to 1 within the confidence set. Parameter estimates (ß) were calculated by summing across the models within the confidence set (weighted by the confidence set model selection probability).

	Idate	**P-food**	**P-2nd neigh**	**Brood size**	***K***	**AICc**	Δ_i	w_i
AICc best				I	1	73.69630	0	0.191
			I		1	73.71439	0.018	0.189
	I				1	73.93930	0.243	0.169
		I			1	74.06800	0.372	0.158
			I	I	2	75.96817	2.272	0.061
	I		I		2	76.36445	2.668	0.050
	I			I	2	76.49656	2.800	0.047
		I	I		2	76.50822	2.812	0.047
		I		I	2	76.52617	2.830	0.046
	I	I			2	76.77466	3.078	0.041
Selection probability	0.307	0.293	0.347	0.345				
ß	-0.033	-0.02	-0.052	0.052				

Appendix 10. Models and parameters from the 95% confidence set for analysis j: asymptotic mass ~ habitat principal components 2 + 3 + 5 + brood size, (n = 16). The table indicates the parameters included in the model, the number of parameters (*K*), the AICc, delta weight (Δ_i ; difference between the AICc of the given model and the AICc best) and the model selection probability (w_i). The latter we recalcualted to sum to 1 within the confidence set. Parameter estimates (ß) were calculated by summing across the models within the confidence set (weighted by the confidence set model selection probability).

	PCA2-habitat	**PCA3-habitat**	**PCA5-habitat**	**Brood size**	***K***	**AICc**	**Δ_i**	**w_i**
AICc best			I	I	2	45.234	0.000	0.580
		I	I	I	3	48.568	3.335	0.110
	I	I		I	3	48.592	3.359	0.108
		I			1	48.792	3.558	0.098
				I	1	51.225	5.991	0.029
			I		1	51.658	6.425	0.023
Full model	I	I	I	I	4	52.139	6.905	0.018
	I				1	52.244	7.010	0.017
	I	I			2	52.404	7.170	0.016
Selection probability	0.160	0.350	0.731	0.845				
ß	-0.027	-0.215	-0.459	0.524				

Appendix 11. Models and parameters from the 95% confidence set for analysis k: asymptotic mass ~ bird community (competitor) principal components 2 + 4 + 5 + brood size, (n = 16). The table indicates the parameters included in the model, the number of parameters (*K*), the AICc, delta weight (Δ_i ; difference between the AICc of the given model and the AICc best) and the model selection probability (w_i). The latter we recalcualted to sum to 1 within the confidence set. Parameter estimates (ß) were calculated by summing across the models within the confidence set (weighted by the confidence set model selection probability).

	PCA2-competitors	**PCA4-competitors**	**Preds**	**Brood size**	***K***	**AICc**	Δ_i	w_i
AICc best	I	I			2	44.101	0.000	0.328
	I	I		I	3	45.309	1.208	0.180
	I				1	45.315	1.215	0.179
		I			1	47.420	3.319	0.062
	I	I	I		3	47.607	3.506	0.057
	I			I	2	47.807	3.706	0.051
		I	I		2	48.020	3.919	0.046
		I		I	2	48.087	3.986	0.045
	I		I		2	48.567	4.466	0.035
			I		1	50.165	6.065	0.016
Selection probability	0.843	0.688	0.171	0.306				
ß	0.437	-0.329	-0.037	0.080				

Appendix 12. Models and parameters from the 95% confidence set for analysis 1: asymptotic mass ~ exposure + entrance area + cavity floor area (Cavity area) + brood size, (n = 38). The table indicates the parameters included in the model, the number of parameters (*K*), the AICc, delta weight (Δ_i ; difference between the AICc of the given model and the AICc best) and the model selection probability (w_i). The latter we recalcualted to sum to 1 within the confidence set. Parameter estimates (ß) were calculated by summing across the models within the confidence set (weighted by the confidence set model selection probability).

	Exposure	**Entrance area**	**Cavity area**	**Brood size**	***K***	**AICc**	Δ_i	w_i
AICc best	I				1	67.544	0.000	0.326
	I			I	2	68.137	0.593	0.243
	I	I			2	69.391	1.848	0.130
	I		I		2	70.062	2.519	0.093
	I	I		I	3	70.690	3.146	0.068
	I		I	I	3	71.364	3.821	0.048
	I	I	I		3	72.322	4.779	0.030
		I			1	72.861	5.318	0.023
				I	1	72.935	5.391	0.022
			I		1	73.320	5.777	0.018
Selection probability	0.937	0.268	0.189	0.381				
ß	-0.474	-0.044	0.013	0.098				