

Abstract

Many bird species are declining in population size. There is a limited understanding of how birds and specifically secondary cavity nesting species select their nest sites. In many cases secondary cavity nesters (SNCs) are thought to be at risk due to limited available nest sites. This study investigated the effect of environmental conditions on nest site selection for the vulnerable yellow-shouldered parrot (*Amazona barbadensis*). Temperature was not found to have a significant influence on clutch size, hatchability or fledging numbers but did have an effect on overall breeding success. Hotter nests at the coldest point of the day were more successful than those nests that had never produced chicks. This information improves our understanding of nest site selection in *A. barbadensis* and provides a good foundation for understanding what cavities may be regarded as suitable for nesting on Bonaire. This information has the ability to influence nestbox design for both *A. barbadensis* and other members of the highly endangered Amazon genus.

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1. Introduction

Maximizing breeding success is the goal of all species yet understanding the mechanisms that drive the associated processes often remains elusive. Birds have been the subject of a multitude of studies on this topic and resultantly are one of the most well documented groups in ecology. This is partly because their life-history strategies can be clearly partitioned into distinct phases. Nest site selection is a conduit to breeding success and thus is one of the more critical phases in their reproduction. Understanding the mechanisms that control nest site selection is a crucial step in devising suitable conservation plans for at risk species.

Unfortunately nest site selection in birds is complex and hard to quantify. The subject is of most relevance for those birds with highly specific nesting criteria and hence least ability to adapt to change. Those most affected often fall into the category: secondary cavity nesters (SNC). They have highly specified criteria with respect to where they

breed and it has become clear that variables like, habitat quality, food abundance, predation risk and environmental conditions are important (Ost, Wickman et al. 2008). The difficulty lies in quantifying the role of these factors within the nest site selection process and ultimately the relative importance of each factor. It remains a key yet underdeveloped field in conservation because without the knowledge of how to alleviate nest site limitation for highly selective species, reducing the risk of extinction is going to be challenging.

The vast majority of parrots are SCNs and with 37% (137 of 374) of species listed as near threatened (41), vulnerable (48), endangered (33) or critically endangered (15) parrots are one of the most imperilled families in the class aves (Birdlife 2010). The majority of parrots are believed to be nest site limited primarily due to the impacts of habitat destruction and are a family in urgent need of conservation (Snyder et al. 2000). *Amazona barbadensis*, the study species of this study, has the dubious distinction of belonging to the most endangered *genus* in parrot family the *Amazona*. Birdlife International have categorised 59% (19) of the genus *Amazona* as either threatened or near-threatened by extinction and within the Caribbean an unfortunate 11 out of 13 species fall under the same categories.

A. barbadensis is listed as vulnerable on the red list and is worthy of conservation attention by virtue of having a high risk of extinction. is poached heavily in parts of its highly fragmented range and chicks are regularly taken by feral cats (Sanz and Rodriguez-Ferraro 2006). The population on Bonaire is known to have a worryingly low breeding population estimated at 21.5% (Williams S, 2009) and is potentially nest site limited. The low numbers of breeding adults certainly reduces the resilience of the Bonairian population to any outbreak of disease or other stochastic event. Primarily however, this study will directly improve the knowledge of nest conditions of *Amazona barbadensis* on Bonaire and hopefully illuminate what may be driving or limiting nest site selection by revealing optimal breeding conditions. The study will provide information that will be relevant to nest box design which should help to improve the conservation status of *A. barbadensis*, which must be the ultimate goal.

This makes *A. barbadensis* an excellent study species and analogue. The results of the project should allow comparisons to be made across the genus and if appropriate across

the *psittascene* family. Furthermore, an improved understanding of how environmental conditions, particularly temperature, affect life-history trade-offs will be essential for conservation on a species level for and more broadly to help predict the effect of global climate change on avian reproduction (McCarty 2001a).

Furthering the understanding of nesting requirements and preferences for *A. barbadensis* will improve identification of suitable nesting habitat and individual nest sites. Further understanding will facilitate policy decisions regarding land use and shape conservation management strategy. The results will be directly relevant with respect to *A. barbadensis* on Bonaire and its wider geographical range and acting as an analogue in increasing specificity for altricial secondary cavity nesting birds, parrots in general and in particular of the genus *Amazona*.

Nest boxes constructed with similar dimensions to that of known nests have been placed in popular nesting areas across the island and have as yet remained unused, except on occasion by the European honeybee (*Apis mellifera*) (*Pers. Obs.*). Parrots can be difficult to persuade to use nest boxes (Sanz et al. 2003, Tatayah R.V.V et al. 2007) which presents a conservation challenge as nearly all parrots are secondary cavity nesters. The role of environmental effects upon breeding in birds has been well studied and yet the environmental conditions of nest sites in the wild have remained a relatively unstudied subject.

1.1 Aims and objectives

The aim of this study was to improve understanding of what influences nest site selection for *A. barbadensis* on Bonaire and what impact differing conditions have on breeding success. The results will be useful for improving conservation management policies and practice for *A. barbadensis* on Bonaire as well as for other analogue species, whether they are parrots of the Genus *Amazona* or any SCN for which this study is relevant. It will also make suggestions on methodology and suggestions for further studies and similar work in the future.

1.2 Objective 1: Nest conditions

Identify most important environmental aspects of nest site selection for *Amazona barbadensis* on Bonaire.

H₁

Nest temperature will be higher than the ambient temperature

H₂

The relationship between nest temperature and ambient temperature will vary between nests

1.3 Objective 2: Breeding

Using data from 2009 and 2010 update the breeding statistics for *A. barbadensis* on Bonaire

1.4 Objective 3: Affect of temperature

Do the environmental conditions of the nest affect breeding success? Investigate how nest conditions affect clutch size, hatchability, fledging number and overall nesting success.

H₃

Nesting success will be higher in the nests that show less variability in temperature

1.5 Overview of thesis

Chapter 1: Introduction to topic and outline of project containing aims objectives and hypotheses

Chapter 2: Presents an overview of the literature and a critical review of previous studies related to nest site selection in SCNs and the factors that are known or hypothesised to affect the parameters of breeding success such as clutch size, hatchability and fledging success. This chapter will build the rationale for the study using existing literature and identified gaps in the knowledge on the topic

Chapter 3: Details the methods and data analysis

Chapter 4: Presents the results found

Chapter 5: Discussion of the results in context of previous studies. Presentation of the strengths and limitations of the project. Suggestions for future work and benefits to conservation

2. Background

Defining the factors that contribute to or detract from breeding success in birds is important because it enables a better understanding of the different life history strategies and population dynamics to be better understood.

2.1 Breeding in birds

It is easiest to tackle this subject in three stages:

2.1.1 Egg production and Clutch size

The most commonly used breeding parameter to represent egg production and the associated costs is clutch size. Clutch size and egg size are products of the egg production mechanism and has been recognised that high quality birds lay more and larger eggs than their conspecifics (Williams 2005). Clutch size can be defined as the total number of eggs that reach the end of incubation (Koenig 1982). This would exclude counts of eggs that are cracked, abandoned or taken by a predator from an experimental point of view.

How life-history strategy controls clutch size is not completely clear or agreed on (Cooper, Hochachka et al. 2005). There are examples of clutch size being affected by temperature, female age, quality and condition, density, territory size and latitude (Hogstedt 1980; Cooper, Hochachka et al. 2005) and clutch size has been shown to decrease in response to low temperatures, high predation risk and latitude (Cooper, Hochachka et al. 2005; Kleindorfer 2007; Salvante, Walzem et al. 2007) .

Multiple theories exist regarding the factors that determine clutch size and each attempt to encompass the theory has been rigorously tested on announcement. Listed is a summary of the major theories and some criticisms of their relative merits:

- i. **Reproduction – survival trade off hypothesis**
This theory states that females that allocate more energy toward survival must allocate less toward reproduction (Stresemann 1927 and Moreau 1994 *in* Cooper, Hochachka et al. 2005)
- ii. **'Lack' clutch hypothesis**
States that clutch size is constrained by the amount of food that parents can bring back to their nestlings as a result of varying day length, varying seasonality or varying predation rates (Lack 1947).
- iii. **Physiological constraints hypothesis**
Life histories are constrained by physiological elements. Endocrine control mechanisms can produce incompatible physiological states that restrict life histories to a single dominant axis of variation (Ricklefs and Wikelski 2002).

The first two theories can be broadly categorized as stating that environmental conditions are the only thing that controls clutch size (Haywood and Perrins 1992) and the first two theories fall into this line of thought. Their major assumption is that clutch size is not limited physiologically, or at least not sufficiently to be impacted selectively (Cooper, Hochachka et al. 2005). Testing of this theory has led to a wide range of brood manipulation experiments which have shown that birds can rear more young than the number of eggs they lay by choice (Monaghan and Nager 1997; Sanz and Grajal 1998). Such findings then prompted a search for negative effects of increased effort on future reproduction (Monaghan and Nager 1997).

In indirect support of the theory, recent studies have shown that the demands of laying and incubating eggs, generally omitted from experiments, could affect parental fitness (Monaghan, Nager 1997) and if Lack's hypothesis is extended to encompass the full demands of producing and rearing the brood it will certainly be more accurate but the physiological constraints hypothesis also has strong evidence against unlimited clutch size via a different route (Wingfield, Visser et al. 2008). It has been demonstrated that inter-individual variation in clutch size can be controlled during the laying and incubation phases with temperature playing an important role (Cooper, Hochachka et al. 2005). Above all it is clear that no one theory is all-encompassing and a combination

of physiology, pertaining to endocrinology, and ecology is required for a more complete understanding (Wingfield, Visser et al. 2008)

2.1.2 Incubation and Hatchability

The energetic costs of incubation have recently received more attention as Initially the impact of the selective cost of incubation was thought insignificant when compared to egg production and feeding the brood (Monaghan and Nager 1997) but it is now clear that this is not the case. Incubation has been shown to significantly affect nest success, female condition (Rastogi, Zanette et al. 2006) Gustavo et al. 2007) and apply selective pressure to clutch size (Reid, Monaghan et al. 2000).

Due to heating and cooling properties of clutches and the subsequent impact on the on-nest off-nest incubation requirements, optimal clutch size might depend on ambient temperatures (Reid et al. 2000). Reid et al. (2000) showed that starlings (*Sturnus vulgaris*) with artificially enlarged clutch sizes (within natural ranges) had lower hatchability and theorised that this was because the clutch size altered the microclimate of the nest and increased water loss, which is known to affect hatchability negatively, which would be of particular relevance in hot arid environments such as Bonaire.

Most bird eggs require incubation because embryos generally develop optimally between 36 °C and 40 °C and development is suspended at temperatures below ~24-26 °C, also known as physiological zero (Cooper, Hochachka et al. 2005). The affect of small temperature changes can have large impacts upon breeding success as can be seen in the fowl (*Gallus gallus*) where a reduction of 1-2°C can increase the length of incubation by 1-2 °C days but any reduction or increase of a further 1-2 °C causes mortality of embryos before they hatch (Romanoff, smith & Sullivan 1938 in Deeming et al.). This shows that maintenance of proper egg temperature is critical as egg temperature levels affect rewarming costs for females and developmental conditions for embryos (Olson et al. 2006).

Mockingbirds (*Mimus polygottus*) with artificially heated nests were able to spend more time off the nest foraging and those provided with additional food but no nest heating were able to spend less time foraging and more time incubating, in both cases improving female condition (Gustavo et al. 2007). The nests of song sparrows (*Melospiza melodia*) provided with extra food were predated less because they

remained unseen due to reduced foraging (Rastogi et al 2005). In both of these examples the influence of environmental conditions on the incubation behaviour is clear.

The hatchability of a population or species is not generally thought of as particularly informative regarding incubation behaviour although it is certainly affected by poor or impaired incubation and clearly no incubation equals zero hatchability. Hatchability is defined as the percentage of viable eggs that hatch; a viable egg defined as one that survives to the end of incubation (Koenig 1982) and traditionally is a measure of the genetic health of the embryo inside the egg. Koenig's (1982) study estimates average hatchability at 90.6% in bird species (n= 113) on average and this figure is seen to be much lower in species that have endured severe bottlenecks in populations size such as the Puerto Rican parrot (*Amazon vittata*) at 70.6% and Kakapo (*Strigops habroptilus*) at 35% (Beissinger, Wunderle et al. 2008). A strong linear relationship between bottleneck severity and reduction in hatchability has been established but environmental conditions are not thought to directly affect it. Indirectly, of course limited food supply for example, may affect the quality adult and eggs (Hogstedt 1981).

2.1.3 Rearing chicks to independence and Fledging number

It is clear by now that beneficial conditions at one stage of the breeding process are to some extent dependent on one another and certain environmental conditions can confer increased fitness down the line (although perhaps not for both chicks and parents). Without successful egg production or incubation there is no fledging yet the relative importance of each stage is almost impossible to quantify. A central idiom of life history theory states that the higher the fecundity the higher the costs for the adults and it has been shown in some birds that the largest energy expenditure occurs at the brood rearing stage and it is often regarded as where the largest cost for the parents lie (Wright, Both et al. 1998). In manipulated blue tit (*Parus caeruleus*) nests there was a 54% decline in adult mortality of females that had to feed 15 chicks compared to those with 3 (although males were relatively unaffected) (Nur 1984). Counter-intuitively, a study on Starlings (*Sturnus vulgaris*) showed there was not the expected loss of adult fitness or the predicted increase in energy expenditure for the pairs with manipulated larger broods who reduced their time spent in and around the nest enabling them to

make more trips with increased food load (Wright, Both et al. 1998). These results show that again it is a complex field and pinning down a central theory is troublesome.

The impact of environmental conditions, such as extreme temperatures, on food supply, individual fitness and suitable habitat, clearly has a strong influence on population decreases or increases sizes of the dependent species (Parmesan et al. 2000) but this is a rather broad view and more specifically this may be distilled to nestling birds facing a trade-off between devoting energy to growth or to thermoregulation (Dawson, Lawrie et al. 2005) and unsurprisingly warmer nests have been shown to confer fitness benefits for the chicks and adults (Dawson, Lawrie et al. 2005; Perez, Ardia et al. 2008; Ardia, Perez et al. 2009). Food supply clearly has an important influence on fledging success and studies that provide supplementary feeding have shown it to increase fledging number and confer other fitness advantages (Hogstedt 1981; Zanette, Clinchy et al. 2006).

2.2 Nest site selection in birds, why a priority?

Nest site selection is the conduit to future breeding success and *a priori* it should be the driver behind nest selection. Many variables have been shown to affect nest site selection such as nest orientation (Ardia, Perez et al. 2009), predation causing an evolutionary change in nesting niche (Brightsmith 2005) and competition from introduced starlings forcing eastern bluebirds into smaller cavities (Pinkowski 1976). Experimental studies that can quantify the effects of a particular variable in relation to another are very limited in supply and the preferences of many species are known from observing shared traits between occupied nests. This is not the same thing as a definitive understanding of the selection process.

Lack of detail regarding the specific mechanics of nest site selection is almost certainly a product of the subject matter. Every cavity, whether because of location, physical dimensions or external influences is different from another in some way and understanding how it appears to the prospective nester is not an easy task. It is often assumed that in selecting a nest site a bird has complete knowledge of the various risks yet it is possible they are not able to assess all the risks appropriately (Ost, Wickman et al. 2008) which is hard to consider meaningfully into experimental design. It is

important to state that a definitive understanding is not necessarily the goal within ecology as once core attributes are identified it is likely these will be sufficient in mounting a successful conservation response in many cases. It is these core nest site selection processes that are still unknown in many species (Cornelius, Cockle et al. 2008). With respect to this study it is sensible to focus on a particular category of birds: cavity nesters.

2.3 Cavity nesting species, limitations and conservation

Secondary cavity nesters (SCNs) require an excavator such as a woodpecker to create a suitable cavity or rely on naturally formed holes in trees or cliffs to nest (Newton 1994). In undisturbed mature habitat this dependence does not appear to be significant as numerous apparently suitable empty cavities lie unused within the breeding ranges of many SCNs (Cornelius, Cockle et al. 2008).

It will come as no surprise however, that in reality many SCN do face nest site limitation (Newton 1994; Beissinger 1996; Sanz 2006). In recent decades the global reduction of pristine habitat and impacts of anthropogenic influence has had a strong negative effect on species with such a strategy (Pimm and Raven 2000; Harris, Jenkins et al. 2005). Haney et al. (2001) The decline of SCN birds as a specific category has been seen over the last 50 years in the Southern Appalachians (Haney, Lee et al. 2001) and within the family most relevant to this study, the *Psittaciformes* of which the vast majority are SCN, there are multiple examples of serious population declines, (Beissinger, Wunderle et al. 2008) and even extinction over the last few decades (Juniper and Yamashita 1990).

If suitable nesting areas are unavailable or decreasing there will be negative effects on a population, ranging from the use of unsuitable nest sites to extirpation of that population from an area completely (Juniper and Yamashita 1990, Collar and Juniper 1992). The scarcity of nest sites, relative to that of open nesting species, amplifies the effects of the classic anthropogenic threats such as habitat destruction (Collar and Juniper 1992), hunting (Thiollay 2005), poaching (Sanz et al 2003), predation (Marshall S.D. 1989), invasive species and competition (Pinkowski 1976) which places cavity nesters under threat as a conservation priority.

Once the selection criteria for choosing a cavity as a nest is understood or can be anticipated, conservation for a species can be targeted effectively and economically

toward what is limiting a population (Jones and Swinnerton 1997). The use of nest boxes and reparations of damaged nests was a crucial element in the recovery programme for the now famous recovery programme for the Echo parakeet and Mauritian Kestrel (Jones, C. G. and K. J. Swinnerton 1997). The provision of additional nesting sites and reparations of damaged nests has been successful at increasing nesting in other studies also (Newton 1994, Sanz et al. 2003) and has led to policy changes such as leaving dead trees standing in plantations and areas of forest under active management and is an effective way of naturally increasing available nest sites for cavity nesting species (Conner, Hooper et al. 1975; Newton 1994). If a species is without a place to breed conservation action plans are almost certain to fail unless the goal is captive breeding and relocation to an alternative area, which should be regarded as a last resort in any case (Snyder, Derrickson et al. 1996). It must be recognised however that nest site limitation is rarely going to be the sole threat requiring amelioration with regards to the limiting factors a species faces and more commonly multiple threats are present (Wright, Toft et al. 2001).

In light of these examples it is clear why SCNs are viewed as important conservation targets. Although highly sensitive to the classic anthropogenic threats, the ability of the conservation manager to provide and monitor additional nest sites is a crucial step to ensuring the survival of a species and improving understanding of the nest site selection process is an integral step in developing specific and effective conservation measures, such as nest box design and placement, which can boost a limited breeding population (Newton 1994, Jones, C. G. and K. J. Swinnerton 1997, Ardia et al. 2006). Nest boxes are commonly used to provide additional nest sites and it is hardly revolutionary to suggest this as a conservation action but, as the conservation crisis deepens, especially for the *Psittascene* family, it is important to recognise the present limitations in general understanding of nest site selection and therefore nest box design and placement (Lambrechts, Adriaensen et al. 2010). Many nest boxes remain empty or are occupied by non-target species (Williams S, 2009, Sanz et al. 2003, *pers.obs*) which if not monitored sufficiently is not only a waste of time and money but could be harmful for the target species by boosting the population of nest competitors.

2.4 How does this study fit within the context of previous work

Relative to the global fascination with parrots and wealth of husbandry and captive breeding information (driven largely by the pet trade) there remains few studies of parrots in the wild. Within those studies very few have focused on environmental conditions within nests. The nest conditions of *A. barbadensis* are not currently known as is the case for the majority of parrots for which there is a general lack of knowledge. Studies investigating the effects of nest temperature have been carried out in tree swallows (Perez, Ardia et al. 2008), starlings (Reid, Monaghan et al. 2000) and northern flickers (Wiebe 2001). Of these studies only Weibe's (2001) focussed on the effects of environmental conditions in nests that were not experimentally manipulated. Understanding the life history of an individual species can reveal much about broader strategies and processes that can be applied widely, especially in a field such as conservation.

2.5 Description of study site

2.5.1 Study Area

2.5.1.1 Geography and Climate

The study was conducted on the oceanic island of Bonaire, Dutch Antilles (288 km²) which lies between 68° 11' - 68° 25' West and 12° 1' - 12° 9' North (Figure #) approximately 87 kilometres north of the coast of Venezuela and 40 kilometres east of Curaçao (DeFreitas et al. 2005). Average annual temperature is 28°C with an average annual precipitation of 463mm, of which 51% falls from October to December (DeFreitas et al. 2005). Bonaire is considered within the 'Caribbean dry region' (Sarmiento 1976) and only in the month of November does the average rainfall reach 100mm (below which evaporation exceeds precipitation in the tropics)(DeFreitas et al. 2005). A strong wind buffets the island from the east (079 degrees) at an average speed of 6.6m/s (DeFreitas et al. 2005)

2.5.1.2 Vegetation

Bonaire the habitat has been dramatically degraded since European colonisation and the introduction of free ranging goats (DeFreitas, 2005). Further habitat degradation results from poachers cutting access holes into tree nests to remove parrot chicks. Most

of the vegetation types can be categorized as secondary. This is considered mainly to be the result of the impact of introduced grazing mammals (principally goats and donkeys) and woodcutting in the past (DeFreitas, 2005).



Figure 1.1. Distribution of Amazona barbadensis (indicated by arrows) across the Southern Caribbean islands of Bonaire (inside red box), La Blanquilla and Isla Margarita and in eastern and western coastal areas of Venezuela, Mainland South America (World Parrot Trust, 2009).

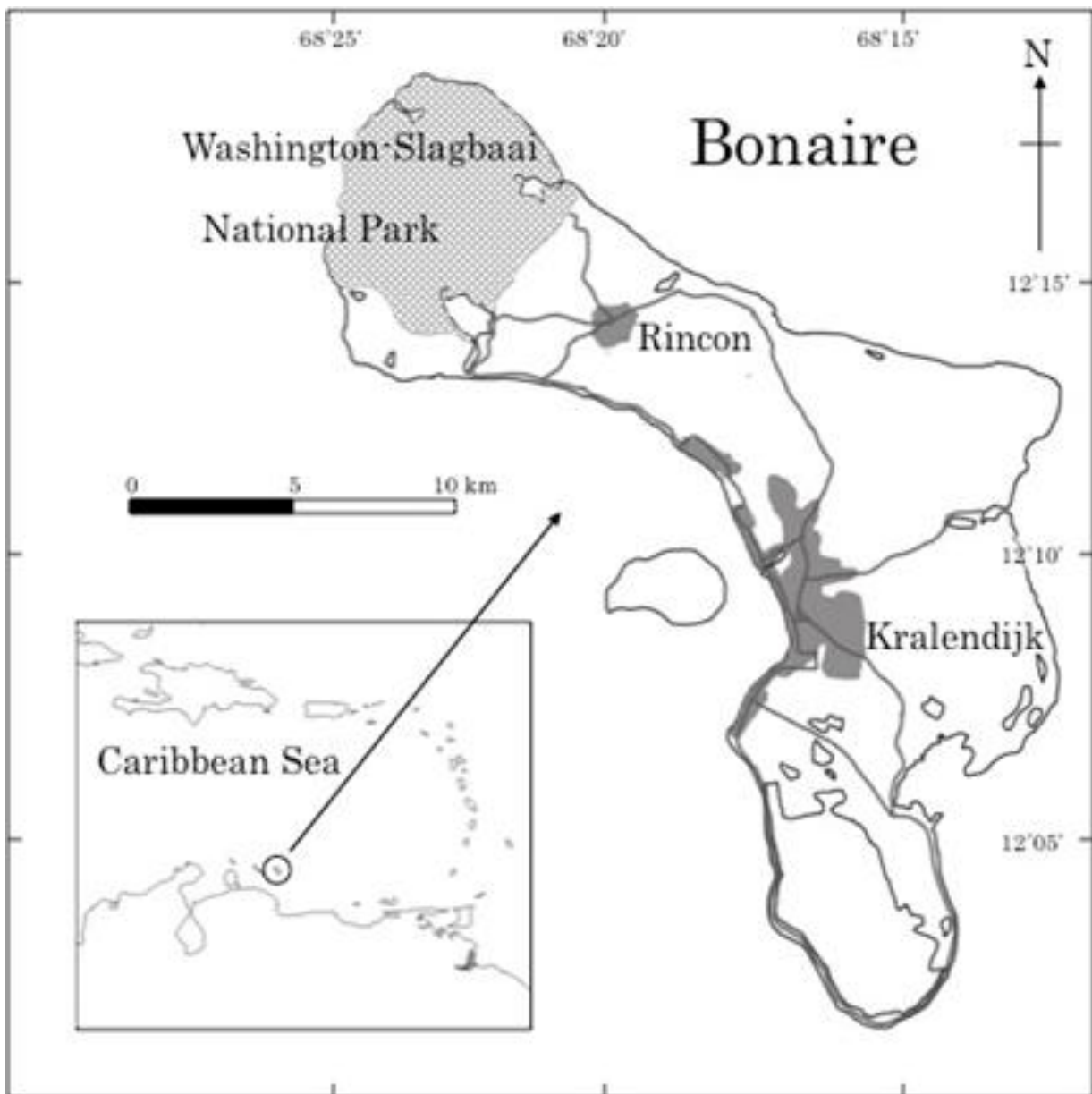


Figure 1.2. Location of Bonaire, Netherlands Antilles, Caribbean. The urban areas of Rincon and Kralendijk are indicated in dark grey and the Washington-Slagbaai National Park is shown in light grey. On Bonaire *Amazona barbadensis* breeds throughout the island in areas north of the capital Kralendijk.

3 Method

3.1 Overview

This chapter will describe, structured by objective, what data was collected, why these data were collected, how they were collected and how they were analysed, including the experimental justification where appropriate.

3.2 Data Collection

Field work was carried out from April 25th to July 10th 2010 although the collection of nest data (environmental and breeding) commenced from the 13th of May because the breeding season started late and the training required to collect the data was fairly extensive and crucial for personal safety. From 2006-2009 breeding data has been collected every year for the population of *A. barbadensis* on Bonaire. This research was carried out by the members of Parrotwatch, an NGO set up by Dr Sam Williams and Dr Rowan Martin. The author joined the team for the 2010 season.

3.2.1 Objective 1: Nest

3.2.1.1 Nests

The temperature, humidity and dew point of the nests was gathered throughout the season using the EasyLog EL-USB-2 Data Logger (DL) manufactured by Lascar Electronics which can take readings simultaneously. The DL's can record data every minute but were set to every five minutes to reduce the size of the data files with no significant loss of granularity in the results. A DL is approximately 3 inches long and half an inch wide making it suitable to insert into most nests without impeding or disturbing the parrots. If it was felt there was insufficient space in a nest to do this so that a parrot would potentially end up incubating it, resulting in inaccurate data, it was not inserted. This assessment was done visually and on the advice of experienced field workers. DL's were inserted into the deepest section of the nest as that is where the chicks would sit. On extraction, data was downloaded directly from a USB port built into the DL. A DL was inserted into every suitable nest so that a 24hr period (running midnight to midnight) could be obtained. *A. barbadensis* nests in both tree and cliff cavities on Bonaire and so equal numbers of each were sampled.

3.2.1.2 Ambient Environmental Data

Ambient temperature (°C) and humidity (%rh) readings were provided by the Metrological Society of the Netherlands Antilles and Aruba (MSNA&A) as average hourly recordings from a weather station based at the airport. Ambient environmental data was required as a control for the nest temperature to account for the nests being measured on separate days. Even though the climate is quite stable on Bonaire the daily

fluctuations in temperature and humidity would have made a comparison of nests on different days experimentally flawed.

The weather station which recorded all ambient data was approximately 10 miles from some of the sampled nests so microclimatic differences between the nest area and the ambient temperature at the weather station were anticipated. To resolve this issue the DL's could have been paired so whilst one was inside the nest the other could have been left in the close vicinity of the nest, more accurately measuring the difference in conditions. Logistically it was not possible because only five DL's were available for the duration of the study. Each nest took approximately 48 hours to sample and sometimes longer so it was too limiting to use two DL's for each nest especially when considering the small size, relatively flat topography and consistent climate of Bonaire.

It was also considered a real practical risk to reduce the useable units of data gathering equipment from five to two. The project rested on the reliability of the measuring equipment and if two DL's were damaged there would have been a severe impact on the project as replacements were not readily available financially or practically. Thus, logistically and experimentally the DL's were used as individual units which enabled five nests to be sampled in 48hrs rather than two. This precaution proved worthy of attention as only 2 of the original 5 DL's remained operational by the end of the field work! Malfunctions mainly occurred near the end of the season; one DL vanished without a trace from an inactive nest, one was accidentally dropped off a cliff and one would not link to the computer having been inserted into a nest.

3.2.1.3 Variables measured and why

For each nest a 24hr period was selected beginning at midnight and ending at midnight. For nests that had two or more 24hr periods to choose from each period was numbered and then chosen at random for inclusion in the analysis. Each 24hr period consisted of 24 data points representing the average conditions of the associated hour to match the ambient data provided.

3.2.2 Objective 2: Breeding data

3.2.2.1 Data collection

Collecting the breeding data ran side-by-side with objective 1. Unlike when inserting a DL, breeding success data was only possible to gather in active nests and once a nest was confirmed it was revisited approximately weekly until fledging or nest failure. Breeding success data was collected from every available active nest.

At each visit to an active nest egg numbers, chick numbers, and various chick development characteristics (which were not used in this study) were recorded. Signs of cracked eggs, predation and poaching events were recorded as these impact clutch size, hatchability and nest success statistics and are also of clear conservation importance from a wider perspective than this project. Chicks were beginning to fledge in mid July just as the allotted time for fieldwork came to an end, an unfortunate impact by the late start to the breeding season, but fledging data has since been relayed from Bonaire as and when it occurred. Breeding data has been collected previously for the years 2006-2009 and the data set from 2010 will be added to it.

3.2.2.2 Variables measured and why

Regular measuring of total eggs laid and brood size enabled clutch size and hatchability to be calculated which, as explained in chapter 2, are important indicators of breeding success and fitness. Weekly nest monitoring was sufficient so that nest or chick failure could be attributed to biological or external factors. Recording fledging number and success was paramount in defining nest success.

Clutch size is defined as total eggs that reach the end of incubation. Hatchability is the proportion of these eggs that hatch. Fledging number is the number of chicks that reach fledging age and nest success is a binary term of whether the nest was successful or not in one chick fledging.

Fledging number was counted two weeks prior to fledging to remove the effect of poaching.

3.2.3 Objective 3: Affect of temperature

3.2.3.1 Data collection

With over 70 known nests (active and historic) nest sampling was prioritized to collect the nests with the most historic breeding data to maximize the statistical power of the study.

It was clear average temperature over 24hrs did not reflect the most important differences between nest and ambient conditions and so lacked biological relevance as an explanatory variable. The coldest and hottest points of the day and the corresponding nest conditions are likely to confer when the most selective pressure would occur on nest site selection as they represent:

- i) when the most damage can occur to eggs and
- ii) when the largest energetic cost to adults will be found through incubation

The temperature difference between the nest and the ambient temperature was converted to a percentage of ambient temperature and was used as the measure of a nests relationship to outside conditions. This relationship that nest has with the ambient temperature was assumed to be fixed and is based on the assumption that that the physical dimensions of a cavity do not change. As an example: a nest at 33°C whilst ambient is 30°C would equal a proportional difference of 10%.

3.3 Field techniques

Locating a nest on a regular basis and accessing it safely whilst causing minimal impact on nesting behaviour was required for the data to be collected successfully.

3.3.1 Locating a nest

Known nests are found throughout the northern half of the island which is less populated and contains Washington Slagbaai (5.543 h²) the only national park on the island. The nests are not limited to one area or habitat type and are found in various sites ranging from cliff faces overlooking hyper-saline lakes to tree cavities in scrub forest. With the knowledge of previous nest sites we made dawn and pre-dusk observations of nest sites. This enabled us to identify the nest sites used by the parrots for 2010. Observations were made using binoculars from a suitable distance as not to affect visibly affect nest prospecting behaviour. Nest prospecting behaviour was easy to

spot as it involved a pair of parrots going into a tree or cliff cavity often for prolonged periods. Allofeeding (feeding between adult birds) between the pair and mating were further clear indicators that eggs laying was imminent.

3.3.2 Accessing the nest

3.3.2.1 Active Nests

Once a nest was identified as active from the observations, access to the cavity was necessary to obtain the environmental and breeding information. Early in the breeding season when the female is still incubating (eggs or small chicks) we were careful not to disturb her on the nest as this has been known to cause abandonment, although rarely. The male calls the female out of the nest for feeding twice a day between approximately 05.45-08:00 and 16.45-19:00. These were the two windows when we accessed the nest causing the least disturbance. Later in the season when the chicks are no longer incubated accessing the nest was less problematic. Cliff nests were generally abseiled to using standard climbing equipment and any chick measurements were done once back on safe ground. Some tree nests required climbing equipment but usually chicks could be pulled out of nests by hand. All nest visitations lasted less than 45 minutes as to reduce stress to adults and chicks. There were no known abandonments during fieldwork.

3.3.2.1 Inactive Nests

Inactive nests could be accessed and logged at any time as there was no risk of disturbing breeding birds. It was possible to log particularly deep nests that were inactive as the DL could be tied to a piece of string and lowered into the cavity.

3.4 Data analyses

In all cases, when assumptions of normality and homogeneity of error variances failed appropriate non-parametric tests were used and in the case of models appropriate error structures specified.

3.4.1 Objective 1

Basic comparative and descriptive statistics were used to show how the nest environment differed or otherwise from the ambient conditions.

3.4.2 Objective 2

Basic descriptive statistics used to show means, distribution and error of data. Data were compared by GLM (see table for error structure) and then TukeyHSD test to see if any years significantly differed from each other or the five year average.

3.4.3 Objective 3

It was not possible to transform the data so that linear models could be used to assess the relationship between breeding success and nest conditions. GLMs with appropriate error structure and link function (see table) were run using R, v2.9.0 (p 511, R Development Core Team, 2009).

Table 3.1. Data structure, error structure, and link function of GLMs used

<i>Response variable</i>	<i>Data type</i>	<i>Error Structure</i>	<i>Link Function</i>
<i>Clutch size</i>	<i>Count</i>	<i>Poisson</i>	<i>log</i>
<i>Hatchability</i>	<i>Proportion</i>	<i>Binomial</i>	<i>logit</i>
<i>Fledging number</i>	<i>Count</i>	<i>Quasipoisson</i> <i>(data was over-</i> <i>dispersed)</i>	<i>log</i>
<i>Nest success</i>	<i>Binomial</i>	<i>Quasipoisson</i> <i>(data was over-</i> <i>dispersed)</i>	<i>logit</i>

For each model the explanatory variable in table # were used and hence represented the maximal model. The minimum adequate model was established using the code below.

```
>model1<-update(model,~.explanatory variable with least significance)
>anova(model,model1, test= "Chi" or "F" (depending on error structure))
```

Table 3.2 Explanatory variables used in GLMs

<i>Explanatory variables for each model:</i>
--

- 1 *Proportional temperature difference at the coldest hour of the day*
 - 2 *Proportional temperature difference at the hottest hour of the day*
 - 3 *Year (data from 2006 – 2010)*
 - 4 *If nest was active when logged(to control for the extra heat of the eggs/chicks/adults in the nest)*
 - 5 *Nest type tree or cliff*
- 6&7** *Interactions between 5 and 1 and 2*
-

4. Results

4.1 Objective 1

4.1.1 Correlation between ambient temperature and humidity on Bonaire

Temperature was very strongly negatively correlated with humidity (Fig.1). The environment on Bonaire is particularly arid and this was not surprising. This result

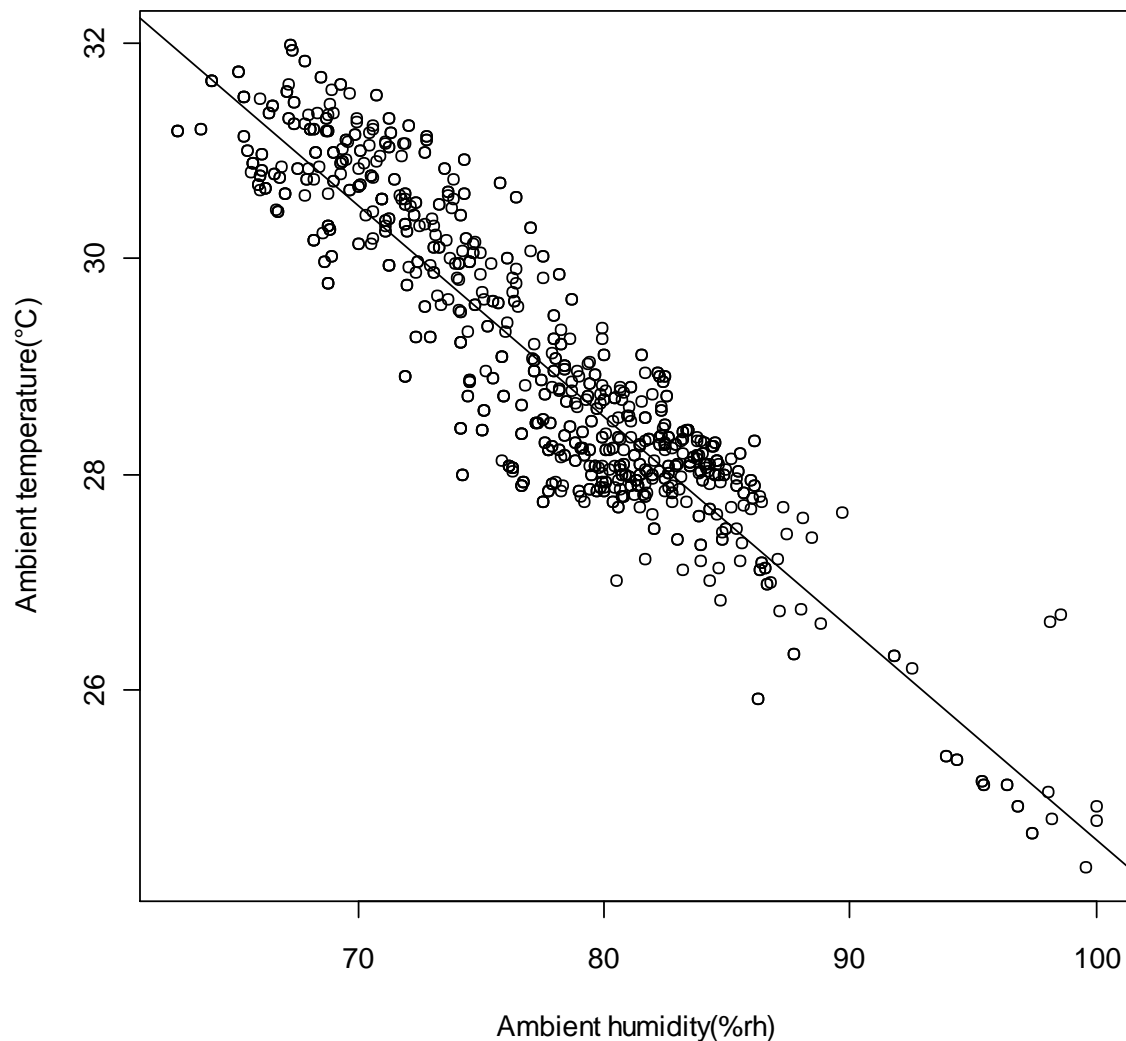


Figure 4.1 Ambient temperature and humidity were very strongly negatively correlated (Pearson's product-moment correlation $r=-0.92$ $t = -66.0266$, $df = 814$, $p\text{-value} < 0.0001$).

enabled temperature and humidity to be considered as one explanatory variable because they were highly likely to explain the same variance in the models. From this point when referring to nest or ambient environmental conditions 'temperature and humidity' will be referred to as temperature unless specified.

4.1.2 Environmental conditions of the nest

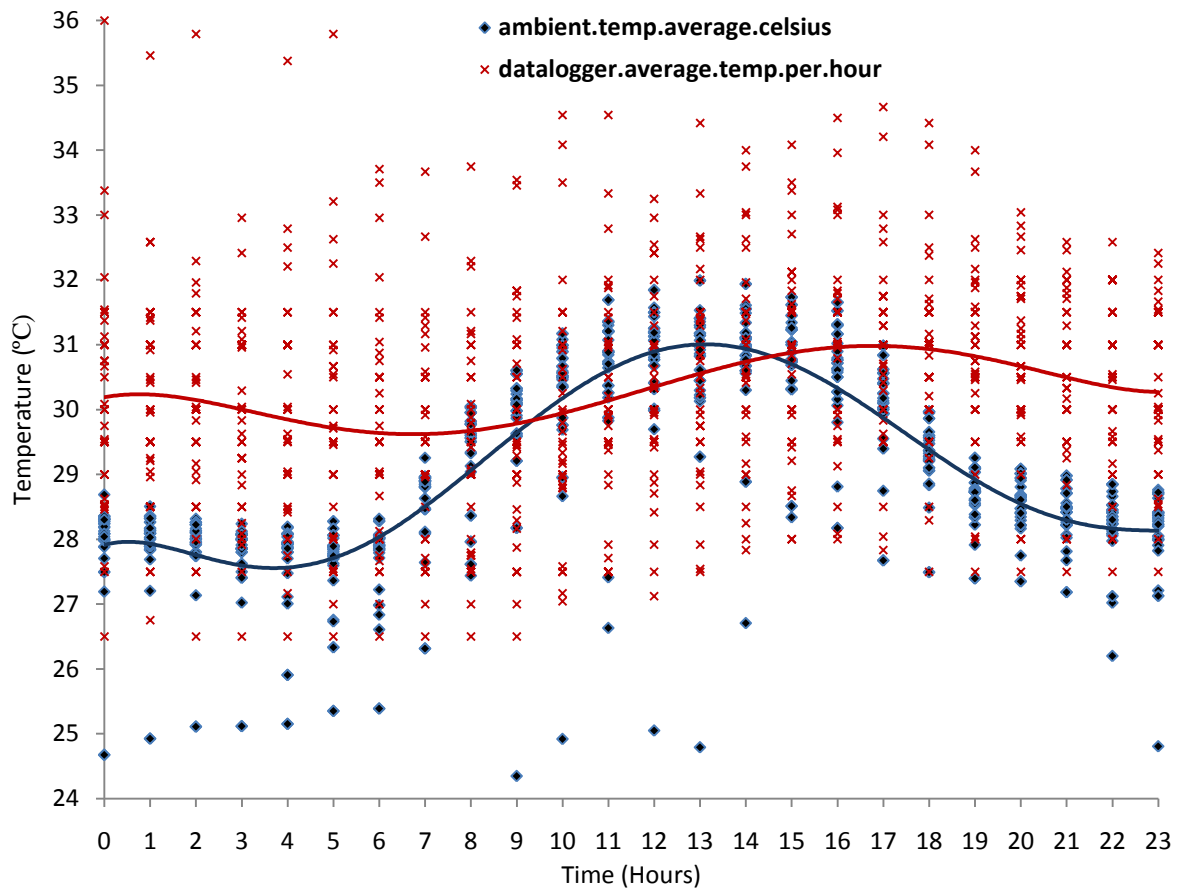


Figure.4.2 Shows the average hourly temperature for all data logged nests ($n=34$) plotted with hourly ambient temperature. The solid red line represents the average nest temperature and blue represents ambient temperature.

It is clear that nest temperatures have more variation per hour than the ambient temperature; approximately 6°C versus 2°C . The range across the whole data set initially appears to be 10.4°C (36.1°C to 26.5°C) but the 6 highest readings all occur in the same nest during the coldest part of the day. There was a clutch in that particular nest (nest 9) and it is almost certainly an example of the DL being incubated by the female parrot. On removal of these points the maximum nest temperature drops to 34.6°C with a range of range 8.1°C .

Over 24 hours nest temperatures average hotter than ambient temperature by 1.2°C (H_1)(Student's T-test, $t = -15.8168$, $P = < 0.0001$) (Table 4.1). Figs. 4.1 & 4.2 show that this is not representative of the relationship however and between the hours of 20:00 and 07:00 the nest is on average 2.3°C hotter than ambient temperature. Conversely between 10:00 and 14:00 ambient temperature is hotter by 0.3°C .

Nests showed a slow rate of heat loss and very effective heat retention, only losing 1.2°C (3.3%) of the maximum average temperature before being ‘charged up’ again over the course of the following day.

Table 4.1 Descriptive statistics for nest and ambient temperature over 24 hours

Description	Nest (n=34)	Ambient
<i>Average(± s.e)</i>	<i>30.3± 0.06</i>	<i>29.1±0.05</i>
<i>Maximum</i>	<i>34.6</i>	<i>32</i>
<i>Minimum</i>	<i>26.5</i>	<i>24.3</i>
<i>Range</i>	<i>8.1</i>	<i>7.7</i>
<i>Standard deviation</i>	<i>1.65</i>	<i>1.45</i>

4.1.3 Biological relevance of relationship between nest temperature and ambient temperature

Only on rare occasion did the ambient temperature drop below physiological zero (~24-26 °C) and this was reflected in nest temperatures never dropping below 26.5 °C. As discussed, using average temperature over 24 hours would not best represent the relationship between nest and ambient conditions for comparison with breeding data.

The most biologically important sections of the day were predicted to be the coldest (4-5am) and hottest (3-4pm) (see *fig 4.3*) as they represented the times when damage to the eggs was most likely to occur. They also represented when the largest incubating constraints would be in effect upon the mothers.

Although temperatures did not appear to increase past the suspected incubation range of *A. barbadensis* (36-42°C) during this study, extremely arid conditions caused by high temperature and thus low humidity would affect the water content of the eggs (ref) which is known to affect fitness and freak temperatures would most like effect eggs and adults the most at the extreme sections of the day.

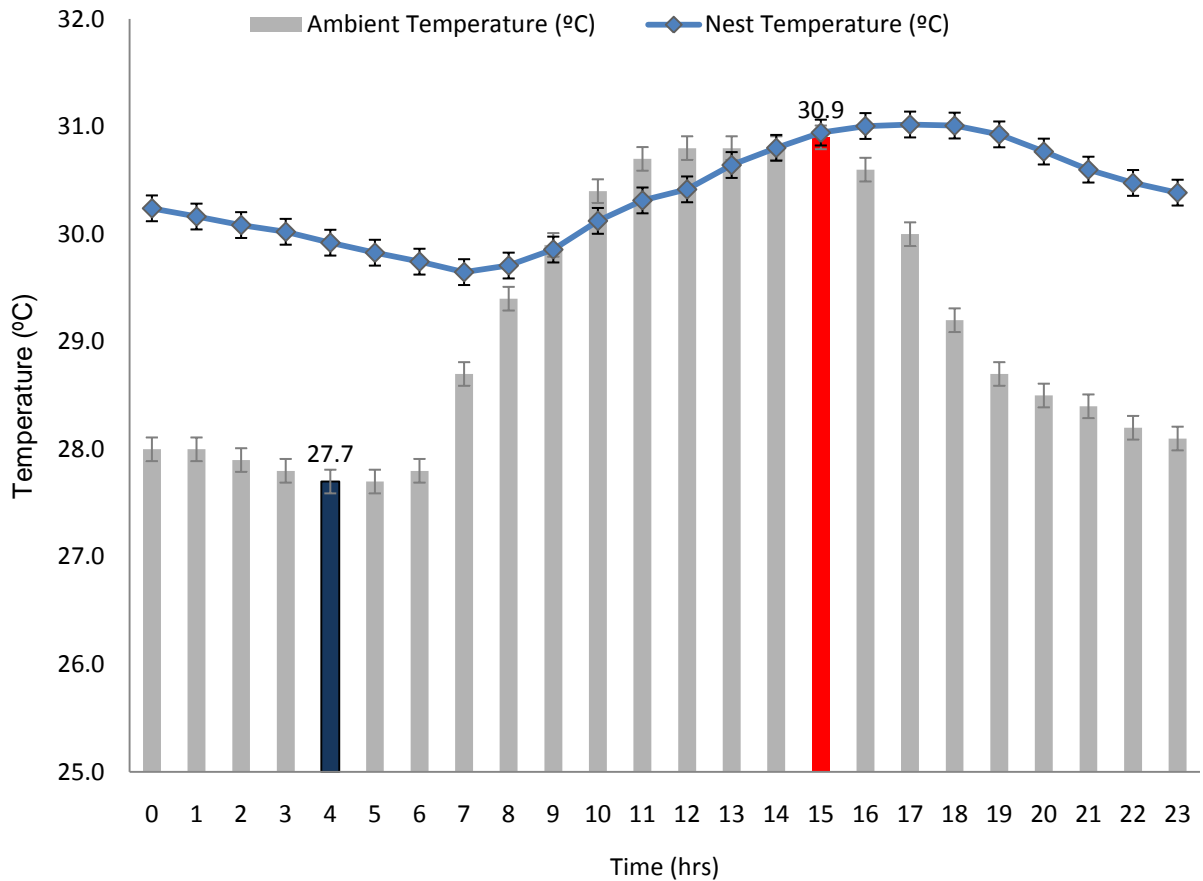
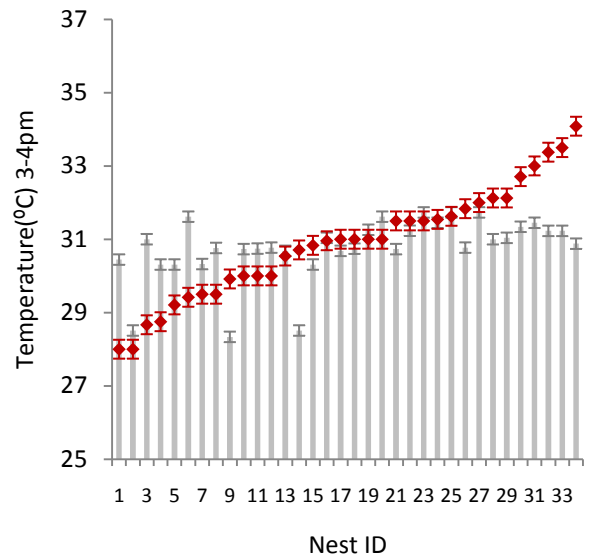
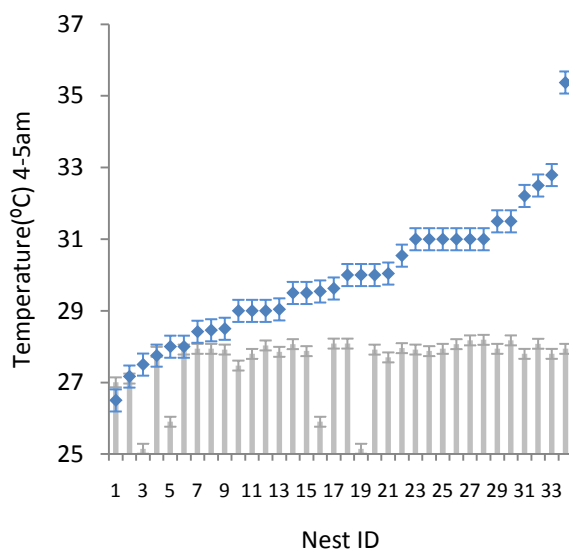


Fig. 4.3 Average ambient temperature and average nest temperature per hour (± 1 s.e.). The coldest and hottest hours of the day are highlighted.

Temperature variation between nests at hottest and coldest point of day

The temperature difference between the nest and ambient varied from nest to nest. Figs 4.4-5 show the how the nests differed from each other at the same point in the day. This was in line with expectations and provided a clear gradient for comparison of breeding data. Fig 4.6 showed that the relative difference of a nest to ambient temperature was not correlated at the hottest and coldest sections of the day justifying the inclusion of both explanatory variables in the models.



Figures 4.4 and 4.5. The blue lines represent nest temperature and bars ambient temperature for each datalogged nest. The first graph represents the coldest hour of the day (4-5am) and the second graph the hottest (3-4pm)(all error bars are ± 1 s.e).

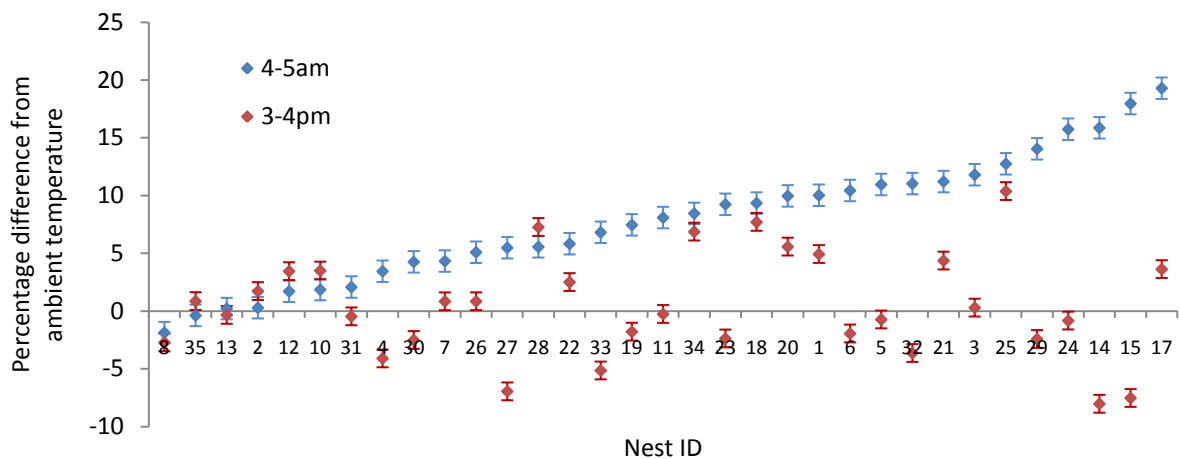


Figure 4.6. Shows the difference in temperature between nests and ambient as a percentage of ambient temperature for all sampled nests (± 1 s.e). There was no correlation between nests that were hotter at the coldest hour of the day and hotter at the hottest hour of the day.

4.2 Variation between tree and cliff nests

Cliff nests were on average hotter by half a degree ($t=4.056, P < 0.0001$) over the course of 24 hours, had a smaller temperature range and higher minimum temperature (see table 4.2) but there was no significant difference between tree and cliff nests regarding the difference between them and ambient temperature.

Table 4.2 Descriptive statistics for tree and cliff nests (± 1 s.e)

	<i>Tree (n=16)</i>	<i>Cliff (n=18)</i>
<i>Average Temperature</i>	<i>30 ± 0.1</i>	<i>30.5 ± 0.06</i>
<i>Minimum Temperature</i>	<i>26.5</i>	<i>27.5</i>
<i>Maximum Temperature</i>	<i>34.7</i>	<i>34.5</i>

4.3 Objective 2

The breeding data for 2010 was fairly typical of previous years but differed considerably with regards to hatchability which dropped to 60% from an overall average of 78% (GLM, $t = -2.033$ $P = 0.044$) and clutch size (3.05) which differed from the previous year (3.7) (TukeyHSD test, $P = 0.032$) but not from the five year average. In absolute terms, of the 64 viable eggs laid in 2010 only 40 hatched which is a very low return relative to other Amazons parrots and birds in general (Williams S. PhD, 2009).

Table 4.3 Summary of all breeding data for *A. barbadensis* from 2006 to 2010

<i>Year</i>	<i>Characteristic</i>	<i>Average</i>	<i>n</i>	<i>Range</i>	<i>Different from 5 year average</i>	<i>Difference between years</i>
2006	Clutch size	3.27±0.23	11	(2-4)	no	no
2007	Clutch size	3.27±0.14	22	(2-4)	no	no
2008	Clutch size	3.29±0.19	17	(1-4)	no	no
					$t = 2.226$ $P =$	
2009	Clutch size	3.7±0.15	20	(3-5)	0.0273	no
						09-10 $P =$
2010	Clutch size	3.05±0.11	21	(2-4)	no	0.032
2006 to						
2010	Clutch size	3.35±0.09	46	(1-5)		
2006	Hatchability	0.79±0.13	11	NA	no	no
2007	Hatchability	0.78±0.09	22	NA	no	no
2008	Hatchability	0.75±0.11	17	NA	no	no
2009	Hatchability	0.75±0.1	20	NA	no	no
2010	Hatchability	0.6±0.11	21	NA	$t = -2.033$ $P =$	06-10 $P =$

					<i>0.044</i>	<i>0.067</i>
2006 to						
2010	Hatchability	0.78±0.06	46	NA		
	Fledge				<i>t = 2.259 P =</i>	<i>06-07 P =</i>
2006	number	2.15±0.34	13	(0-4)	0.02487	0.0374
	Fledge					
2007	number	1.08±0.26	25	(0-4)	no	no
	Fledge					06-08 P =
2008	number	1.04±0.18	26	(0-4)	no	0.054
	Fledge					
2009	number	1.43±0.29	23	(0-4)	no	no
	Fledge					
2010	number	1.28±0.23	25	(0-4)	no	no
2006 to	Fledge					
2010	number	1.26±0.14	58	(0-4)		
	Fledge success				<i>t = 1.655 P =</i>	<i>06-07 P =</i>
2006	Fledge success	0.92±0.08	13	NA	0.099	0.0215
2007	Fledge success	0.52±0.1	25	NA	no	no
2008	Fledge success	0.69±0.09	26	NA	no	no
2009	Fledge success	0.61±0.1	23	NA	no	no
2010	Fledge success	0.72±0.09	25	NA	no	no
2006 to	Fledge					
2010	success	0.63±0.06	58	NA		

Overall nest success on Bonaire from 2006-2010, defined as number of nesting attempts/nests that successfully fledge one chick was 48.1% (s.e ± 0.04, n= 135) which is in line with other Amazon genus. This statistic includes non-biological factors, such as poaching and predation.

4.4 Objective 3

For each response variable the same maximal model was run (see methods for explanatory variables and error structures). All models used for this section of the analysis were GLM's. It is worth noting that n changed depending on the model depending on which data points could be included for that particular breeding parameter. For example, all nests that were not found as eggs (i.e. already had chicks) were not included in clutch size or hatchability models. Nest success was a binary measure of whether a nest had ever been successful and thus n equalled total nests sampled.

4.4.1 Response variable ~ Clutch size

Minimal adequate model (MAM):

Proportional temperature difference at the hottest hour of the day ($n= 92, z = -0.990, P = 0.322$)

The model did not produce significant results or show any trends therefore clutch size was not affected by temperature

4.4.2 Response variable ~ Hatchability

MAM:

Proportional temperature difference at the hottest hour of the day ($n= 92, z = -0.825, P = 0.410$)

The model did not produce significant results or show any trends therefore clutch size was not affected by temperature

4.4.3 Response variable ~ Fledging Numbers

MAM:

Year ($n=59, 2006 t=2.464 P=0.0169, 2007 t= -2.366 P = 0.0180$)

Within the explanatory variable *Year* the factors *2006* and *2007* (representing those years) came out as significant (GLM, $t=2.464 P=0.0169$ and $t= -2.366 P = 0.0180$). This is in line with the breeding statistics as 2006 and 2007 represented the best and second

worst years respectively (see *Table 4.2*). It was surprising that 2008 did not come out as significant also.

4.4.4 Response variable ~ Nest Success

Minimal model:

Proportional temperature difference at the coldest hour of the day (n=34, t = 2.272, P = 0.0269)

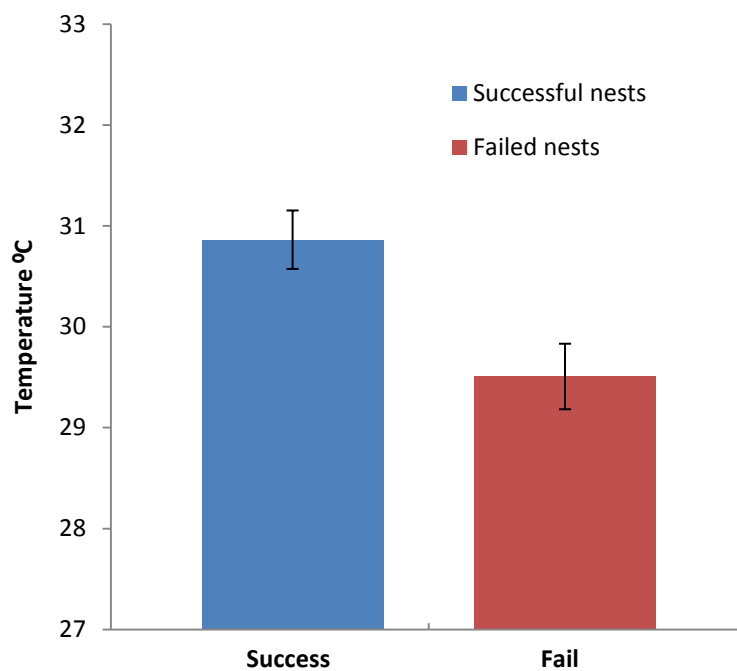


Fig 4.4 The average temperature at 4am for successful nests (n=29) is 30.9°C and for nests that have never been successful (n=5) 29.5 °C (± 1 s.e).

Nests that were hotter at the coldest part of the day were more likely to be successful at raising at least one chick to independence. Figure 4.4 shows the average temperature difference between successful and unsuccessful nests is 1.4°C which is in line with H₃

6 Discussion

5.1 Overview

As predicted, nests on Bonaire were hotter than the ambient temperature for all but a few hours in the afternoon (H₁) and they retained their heat extremely well. There was clear variation in the temperature difference between nests and ambient temperature

which provided a suitable gradient to compare the four categories of breeding success against (H_2). Cliff nests were on average hotter than tree nests by 0.5°C but the two nest types were not found to significantly differ from the ambient temperature relative to each other.

The 2010 breeding success data for *A. barbadensis* was generally in line with previous years (H_3) except for hatchability which had dropped significantly. Average clutch size, although not significantly different from the overall average showed a significant drop in size from the previous year.

Nests from which a chick had successfully fledged from were on average 1.4°C warmer at the coldest hour of the day than nests that had never been successful. The year that the data was collected was significant in explaining fledging numbers in 2006 and 2007. These years represented the most successful and second least successful years on record so this was not surprising but it was unknown why 2008, the worst year on record, was not significant. No other breeding parameters were shown to be affected by temperature. This raised a number of possibilities which will be discussed below.

5.1.1 Results: Objective 1

The data was fairly conclusive in describing the relationship between nest and ambient conditions and providing a comparison of the individual nests.

Nests were hotter on average by over a degree but the difference in temperature was most pronounced when the ambient conditions were coldest. This is not surprising as this period is likely to be the most limiting part of the day upon breeding success and potentially only nests with efficient heat retention would be selected for. Although this may represent the strongest environmental selective pressure exerted by a cavity none of the nests reached the reported physiological zero ($\sim 24\text{-}26^{\circ}\text{C}$) for incubating eggs (Cooper, Hochachka et al. 2005) and ambient temperature only averaged below 26°C for 13 hours in 34 days (24hrs per nest). This suggests that overall the selective pressure exerted by nest conditions may not particularly strong and a large sample size may be needed to detect an influence.

To fully assess the importance of specific temperature ranges on *A. barbadensis* the egg temperatures during incubation needs to be established. As way of an approximate guide to this a professional parrot breeding company suggests when incubating eggs

use a temperature range of 37.1 to 37.8°C and a humidity range of 32-52% for optimal development (Voren H. 2009). Combing this information with the raw data logger readings from nest 9 in which the DL was incubated by the mother (reaching 37°C) would suggest that *A. barbadensis* does not deviate far from the average but *A. barbadensis* has evolved in hot, arid conditions and may have more specific environmental requirements than can be derived from this information. The temperature variation between nests was gradual but very clear and was apparent at both the coolest (4-5am) and hottest sections of the day (3-4pm). The range was over 6°C from the coolest nest to the hottest in both cases and this should have provided a large enough difference for a relationship with breeding success to be detected if one was present.

The results suggested that although cliff nests were 0.5 °C hotter than tree nests there was no significant difference between tree and cliff nests with respect to ambient temperature. The absolute difference between the nest types may have arisen because the temperature was simply hotter on the days when cliff nests were measured. The similarity between the nests is not surprising if particular conditions are required for successful breeding.

There were some limitations that may have influenced the results obtained regarding nest conditions. The data loggers were compared to one another in a pilot study and although no meaningful differences were found between them they were not compared directly to the weather station that recorded the ambient conditions during the project. There may have been a difference between the two types of recording equipment and future experiments of this type need to account for this type of error. It would have been preferable to pair the data loggers (one inside the nest and one outside) so that very accurate indications of the nest and ambient conditions could have been made. This information would also have provided an interesting insight into the climactic variation across Bonaire. As explained in the methods this was not possible and during the fieldwork there were localised rain showers that may have distorted the readings. Finally, it was not possible to place the data loggers in the same position within all nests. The deepest point of the nest, where the chicks would sit, was always the target but this was not always possible and environmental inaccuracies may have occurred as a result although probably minor.

5.1.2 Results: Objective 2

Reproductive parameters for the *A. barbadensis* population on Bonaire are within the expected ranges for Amazon parrots. Of particular interest is the existence of *A. barbadensis* populations based on other islands in the Caribbean (Margarita and La Blanquilla). Comparisons between the islands reveal that clutch size is very similar to that of Margarita island (3.33, n=322) but higher than La Blanquilla (2.24, n=29) (Rodriguez-Ferraro and Sanz 2007). La Blanquilla is drier and has more poaching and invasive predators than Bonaire which may account for the lower clutch size on that island (Williams, S, 2009).

The breeding statistics from 2010 showed a reduction in hatchability and clutch size from previous years. The environmental conditions of nests are not likely to have changed (relative to the ambient conditions) over the course of the last few years and so this data is probably not relevant for this section. Ecological factors may have had more of an impact. 2009 was a particularly dry year with significantly reduced rainfall (see Table. 5.1) (MSNA&A). The brief rainy season that occurs in October and November largely failed to materialise in 2009 and is highly likely to have had a detrimental impact on the fruit and seed production of the vegetation of Bonaire in 2010. Fruit and seeds make up the vast majority of *A. barbadensis*' diet (Williams, S, 2009) and poor nutrition is known to decrease clutch size and the quality of eggs laid (Hogstedt 1981). It is highly likely that in 2010 the breeding population of female parrots on Bonaire were in poor condition pre-breeding season and therefore invested less reproductive effort into that years clutch. Parrots are long lived birds and reproductive effort is likely to be maximised over a lifetime which would lead to reduced clutch sizes in years with bad conditions.

Table 5.1 Rainfall statistics for Bonaire

Year	Rainfall (mm)
2006	1390.7
2007	1009.5
2008	1175.7
2009	720.2
2010*until 3 rd September	681.6

Inbreeding is perceived as the major cause of low hatchability however (Briskie and Mackintosh 2004) and it is known that severe droughts on Bonaire have caused population crashes in the past. The population was reduced to an estimated 100 birds in 1978 (Voous, 1983) which makes it very likely that the population is inbred. The effects of bottlenecks on hatchability has been studied and populations reduced below 150 birds had an average hatchability of 75% which reduces with the severity of the bottleneck (Beissinger, Wunderle et al. 2008). This would explain *A. Barbadosensis*' low hatchability relative to the average for birds (90.2%, (Koenig 1982)). An interesting comparison can be made with the hatchability of *A. barbadensis*' population on Margarita (91.0%) which has not been recorded to have experienced a bottleneck of the same proportions (Rodriguez-Ferraro and Sanz 2007). This is a stark example of what hatchability could be for *A. barbadensis* and other parrots in the Amazon family and provides a clear conservation target for conservation managers.

5.1.3 Results Objective 3

H₄ remains somewhat unanswered. Temperature did not appear to have an effect on clutch size, hatchability or fledging numbers but nests that have been successful were significantly warmer than perennially unsuccessful nests. The effect of temperature has already been discussed with specific reference to clutch size, hatchability, nestlings and adults and in all cases warmer temperatures have been shown to confer benefits (Conway and Martin 2000; Reid, Monaghan et al. 2000; Perez, Ardia et al. 2008; Ardia, Perez et al. 2009). It follows that warmer nests should be more successful and the evidence from this study supports this. With this in mind it is somewhat surprising to see no effect of temperature on any of the separate components of breeding. This may not be uncharacteristic however as the relative importance of each breeding stage is unknown and perhaps indicators of chick health, such as growth rate and asymptotic weight (Wright, Both et al. 1998), are more strongly linked with overall nest success than the characteristics measured in this study. It is logical that the longer a chick has been in the nest the larger the investment has been from the parent. If you assume that the greater the investment the higher the chances of success recording the growth rate of a chick may be a more accurate representation of parental investment and therefore more effective indicator of overall nest success (Coulson and Porter 1985). The growth

rate of chicks has also been shown to indicate parental quality (Coulson and Porter 1985).

Warm nests decrease the probability of a nest reaching threshold temperatures such as physiological zero (Cooper, Hochachka et al. 2005) which may prevent future developmental costs but this may not be as important as the additive value of the nest existing at preferred temperatures over the course of the breeding process (Ardia, Perez et al. 2009). Whichever is more important, it is likely that both mechanisms work together to add considerable benefits. This highlights the lack of knowledge surrounding how each breeding stage relative to each other affects overall success.

As with many ecological studies, a larger data set would have been preferable but it was not possible to insert data loggers into all the nests. There were 67 known nests by the end of 2010 which gives an idea of the possible sample size but it was not possible to access them all. Some had inaccessible nest chambers because they were too deep or had limited space for a data logger to be inserted. If a similar experiment was focused exclusively on the environmental conditions within a nest it would be preferable to conduct the fieldwork when the parrots are not nesting. This would remove the often considerable time spent waiting for the mother to leave the nest every day (during incubation) and remove the temperature effect a brood may have on the recordings. This effect was included in the models but removing it as a possibility is preferable as the affect on temperature at different stages of nesting is not likely to be consistent.

It is known that some parrot pairs return to the same nest each year (Martin R. O 2008) and in a similar species the Blue-fronted Amazon (*Amazona aestiva*) nest site reoccupation was reported as 62% and shown to be positively linked with nest success the previous year (Berkunsky and Reboresda 2009). This presents the issue of autocorrelation within the data as the results from one nest over five years may in fact be the same pair. This is problematic because if one individual was responsible for 5 data points in a data set of 50 it will strongly influence the results relative to its true weighting which will skew the effect of nest conditions toward the reproductive tendencies of that particular parrot. Fortunately this was not a major issue for this study as the significant results were not affected by autocorrelation and the data that this may have been an issue for did not prove significant. Nonetheless this issue needs to be

addressed for future studies of similar nature. A different statistical approach that could control by nest ID would be needed to correct the autocorrelation and a mixed-effect model (p 628, R book) seems to have the functionality to do this, but further investigation is needed. An additional improvement would be to control by pair which would require detailed population knowledge of the breeding population of *A. barbadensis*; possible as the parrots have individual markings that would enable identification.

Repeated samples of nest conditions within a season and across years would provide a basis for testing the assumption that nest conditions are fixed (relative to the ambient temperature) and although the schedule was very tight it would have been beneficial to have carried out repeated sampling on selected nests for this study. Without making this assumption the historic breeding data would not have been useable and that would have made the data set too small for meaningful analysis. The assumption does introduce year effects into the data which cannot really be controlled for using a GLM. Variation between years will occur in vegetation, food supply and predator numbers to name some of the variables and although likely to be similar on an annual basis they will have affected breeding success differently each year. As previously suggested it appears mixed-effect linear models may resolve this problem in future studies.

5.1.4 Suggestions for future work

The affect of temperature on clutch size, hatchability and fledging number for *A. barbadensis* on Bonaire does not appear to be particularly influential. This may be because the explanatory power of these breeding parameters with respect to breeding success *per se* are not as indicative as assumed or that the temperature range on Bonaire is too benign to influence nest site selection as a solitary factor. In both cases other explanatory variables such as chick growth rates and fruit production would potentially be better proxies for what drives nest success and nest site selection. The significant drop in clutch size and reduced hatchability in 2010 were experienced after a particularly dry year and additional reference to the low clutch size found on La Blanquilla (Rodriguez-Ferraro and Sanz 2007) would further support fruit production as a particularly important variable.

There is a good opportunity to resolve whether nest site selection is occurring on Bonaire and consequently reveal insight into the drivers behind nest site selection. There appears to be a surplus of natural cavities that would be suitable as nests on Bonaire (Williams, S 2009, *pers.obs*) yet as mentioned in chapter 2 the term 'a suitable cavity' is not well understood (Cornelius, Cockle et al. 2008). Williams (2009) investigated the physical dimensions of nests and 'suitable cavities' so, by recording the environmental conditions of the cavities (and increasing the sample size for nests) the basis is there for a comprehensive understanding of the nest sites that *A. barbadensis* uses which has clear implications for nest box design, habitat management and nest site selection theory. A recent review has indicated the importance of detail in nest box design for success of individual projects and wider use amongst the conservation community (Lambrechts, Adriaensen et al. 2010).

More broadly there are important unanswered questions about the demographics of *A. barbadensis* on Bonaire such as age structure and sex ratio which may instantly reveal the drivers behind the low breeding numbers which makes the population so vulnerable. The number of breeding individuals within parrot populations is another deficient area within parrot ecology (Matuzak and Brightsmith 2007) and if the resilience of a population is to be understood this sort of information is required.

The island ecology, underdeveloped nature and growing conservation core of Bonaire, provides an excellent framework for developing a detailed understanding of *A. barbadensis* and the drivers behind what is threatening its population on Bonaire and more widely. Furthering our understanding of *A. barbadensis* in the manner outlined will provide evidence for many of the mechanisms that are poorly understood yet critical to successful conservation strategies for cavity nesting species such as nest site selection and the impact of environmental factors on breeding success. With particular relevance for parrots and the genus *Amazona* by improving the knowledge of fundamental questions in bird ecology, with specific examples will provide a springboard that conservation can utilise for some of the most endangered and enjoyed bird species alive today.

6. References

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Appendix A

Pilot study

Comparative study of Data Loggers

To ensure the five DL's were recording temperature alike prior to being inserted into any nests they were placed in a draw inside our accommodation for 24hrs.

Data logger	Average Temp
DL1	29.8
DL2	29.7
DL3	29.9
DL4	29.8
DL5	29.8
(max – min)	0.2

The results confirmed that they could be treated as one.