NESTING DYNAMICS OF THE SCARLET IBIS (*Eudocimus ruber*) IN TRINIDAD, WEST INDIES

By

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ABSTRACT

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Key Words: breeding biology, Caroni swamp, ciconiiformes, colonial waterbirds, *Eudocimus ruber*, human disturbance, Scarlet Ibis, Trinidad, West Indies.

The effect of human disturbance on colonial waterbirds is a global issue. Many colonial waterbirds are migratory, and their protection depends on balancing conservation of their habitats and habits across many regions. Such protection is critical given the economic benefits that come from a growing ecotourism industry, involving bird watching and other recreational activities. This thesis begins with a review of the literature available via Web of Science and Jstor, to determine whether the effects of human disturbance on the habit, behaviour, and physiological characteristics may differ with biome, migratory habit and functional group.

Waterbirds throughout the world suffer from similar effects of human disturbance such as increased vigilance, reduction in feeding rates, lower reproductive success and greater energetic loss caused by destruction and manipulation of habitats. Acclimation to human disturbance can also cause birds to increase their feeding efficiency and tolerate or habituate to such disturbances. Such acclimation may result in positive outcomes. The classification of colonial waterbirds according to biome, habit and functional group is helpful, because food and nesting sites vary, the energy requirement based on habits vary and body size and structure of species differ. Based on the literature reviewed, studies on colonial waterbirds in tropical regions are limited and available research is limited to their wintering or summer home range. Additional research should include the effects of human disturbance in order to understand how it affects the behaviour, physical fitness and physiological characteristics of waterbirds.

Scarlet Ibis (*Eudocimus ruber*) is a significant species of colonial waterbirds in Trinidad, West Indies, whose management is hampered by limited information on its life history. Although a keystone species in the tourism industry, it is under increasing pressure caused by poaching, human disturbance and habitat destruction. The nesting pattern of the Scarlet Ibis in the Caroni Swamp, a traditional breeding area in Trinidad, was studied during the 2008 breeding season, in order to determine factors that may have an influence on its reproductive success.

Observation of key spatial variables in the nesting site such as distance of neighbouring nests, number of nests per tree, nest cover, distance to the water edge, diameter of nesting tree and number of egrets present, was undertaken and related to clutch size, hatching success and fledging success. The number of nests per tree, distance to the water's edge and distance of the neighbouring nests were the most significant factors that influenced breeding success in any or the three measures. Nesting pattern appear to follow the "selfish herd hypothesis" described for the Scarlet Ibis in Brazil by Olmos (2003). Nesting aggregation is one strategy used by birds to reduce the chances of predation.

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I wish to dedicate this thesis to my wife Alana, our daughter Sangeeta and our upcoming addition to our family. When I started this journey, we were just blessed with the wonderful news that we were going to have a baby, and regardless of the distance between us, you supported me in my dream and all my endeavors', and at times when I was ready to quit, you helped me through, and for this, words cannot express the gratitude, love and admiration I have for you, thank you. I also wish to thank our families, for the support and assistance they rendered to us, and for filling the role of husband and father in my absence, your support was priceless. Without such support, this thesis would not have been possible.

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CHAPTER 1, GENERAL INTRODUCTION

Management and conservation of the flora and fauna resources of small tropical island states are critical in ensuring their sustainability. Although tropical forests only occupy about 13% of the earths' land surface, they account for almost 50% of the forest resources extracted globally (Houghton 1990). These forests are also important biodiversity reserves, which we depend on both directly and indirectly, because they provide us with many important goods and services and also help us maintain the life-sustaining systems that make up the biosphere (Birdlife International 2008). However, we are losing this biodiversity very fast, as human consumption and activities continue to expand. According to Birdlife International (2004), human activities have contributed to the destruction of half of the world's natural habitats, and these habitats are important for almost 75% of all species of birds in the world. One such habitat for colonial waterbirds is wetland forest, it accounts for 6% of the worlds' land space and is declining globally (Bellio *et al* 2009). It is estimated that approximately 50% of the world's natural wetlands have been lost since the 1900; most losses occurred in the northern latitudes during the first half of the 20th century, while the sub-tropics and tropics came under greater pressure later (Czech and Parsons 2002).

The major focus of management is to ensure the conservation or manipulation of species that are of special interest to the people in a particular region, especially in tropical habitats, so as to provide a balance between the needs of the human users and the persistence of the species that are important to them. The breeding biology of a species or group of species and the effects of human disturbance is a focus of many management strategy because of wide spread influences of human activities. These have served as a major focal point of many investigations on waterbirds (Blanc *et al.* 2006; Nisbet 2000; Carney and Sydeman 1999; Boyle and Samson 1985).

Waterbirds are a diverse and fascinating group of birds, which comprises over 30 families characterized by their association with water, during a part of or throughout their life cycle. Studies by Birdlife International, which is “a global partnership of conservation organizations that strive to conserve birds, their habitats and global diversity”, indicate that of the 64% of birds that are globally threatened, most species belong to the tropical regions (Birdlife International 2004). According to a 2008 report, many waterbird species are declining and over 17% of these species are considered globally threatened (Birdlife International 2008).

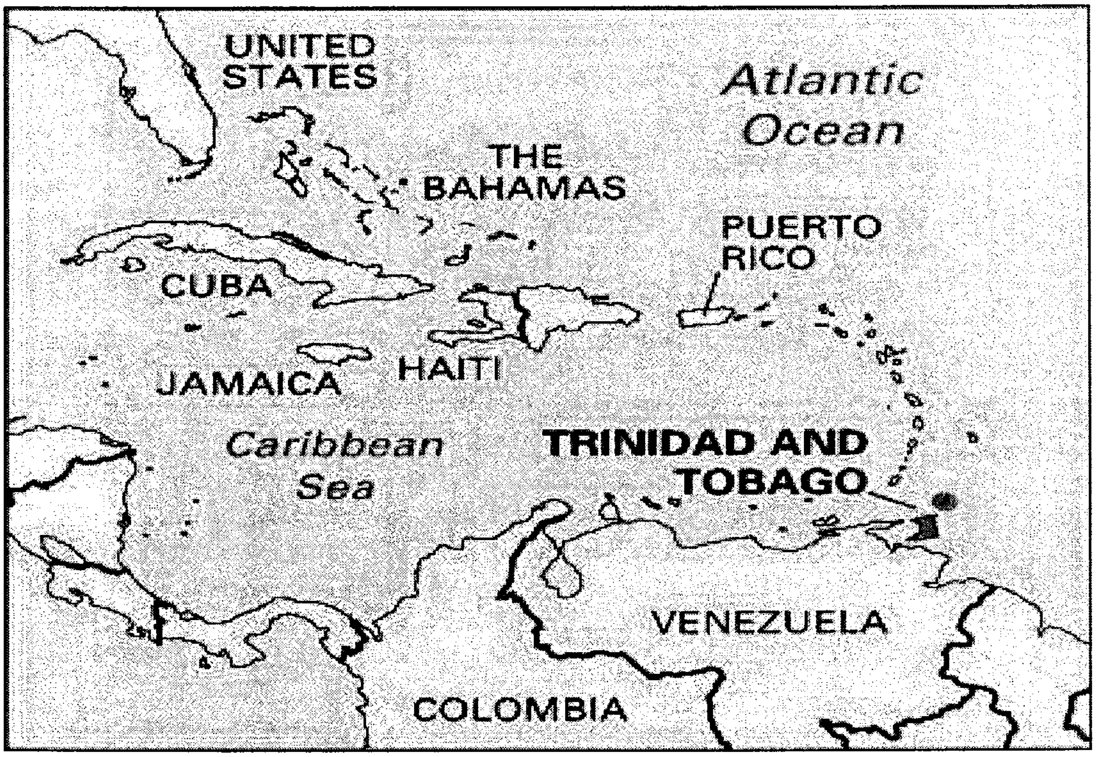
The management and protection of colonial waterbirds must consider not only ecological but also economic aspects, because of their diversity, natural beauty and potential to generate revenue and create employment (Lim and McAleer 2005; Naidoo and Adamowicz 2005; Uyarra *et al.* 2005). Large aggregations and spectacular displays make colonial waterbirds a perfect subject for naturalists and bird watchers. Therefore, they serve as a platform for a thriving ecotourism enterprise. Many times, habitats of colonial waterbirds are limited in space, with little or no alternative habitat available, and as a result, many species are considered “keystone” species in the economy of many small island states. An example is the Scarlet Ibis (*Eudocimus ruber*) in Trinidad and Tobago, West Indies (Bildstein 1990).

Constant increase in human intrusion into tropical habitats makes management of tropical colonial waterbirds a high priority. Unfortunately, most research involving colonial waterbirds has been concentrated in temperate regions. This lack of information, on tropical waterbird species and habitats, forces wildlife managers in small, tropical island states to implement policies and procedures that were developed for temperate species. This issue raises the question of whether small island states can properly manage increased human presence caused by ecotourism and recreational activities with information borrowed from elsewhere. This question is the motivation for this study, which focuses on the twin islands state of Trinidad and Tobago, and more directly on the Caroni Swamp in Trinidad, which is home to one of the country's national bird, the Scarlet Ibis. This bird has been one of the most important species in the country ecotourism industry.

TRINIDAD AND TOBAGO

The Republic of Trinidad and Tobago has been publicized as "the land of hummingbirds, steel pan and calypso," due to the diversity of hummingbirds, the invention of the steel pan (Rossing *et al.* 1996), the only new acoustic musical instrument invented during the twentieth and twenty-first centuries to date, and the popularity of calypso music (Liverpool 1994). This island state is a nation in the southern Caribbean Sea that possesses a wealth of native flora and fauna, because of its location in the most southern islands of the Lesser Antilles, and its proximity just off the northeast coast of South America, about 11 km from the Venezuelan coast (Figure 1.1).

Figure 1.1. Location of Trinidad in relation the Central and South America



It is an archipelago state that comprises two separate larger islands and 21 smaller islands. The larger of the two main islands is Trinidad, which is considered the commercial and industrial centre and comprises 4,768 km^2. The smaller main island is Tobago, which is considered a tourist destination and comprises 300 km^2. Both main islands have a landscape of mountains and plains and a tropical climate with two seasons, a dry season during January to May and a wet season during June to December. Trinidad and Tobago has a population of approximately 1,214,000 and its economy is built around oil and asphalt mining and refining, followed by agriculture and forestry (Mahy 1997).

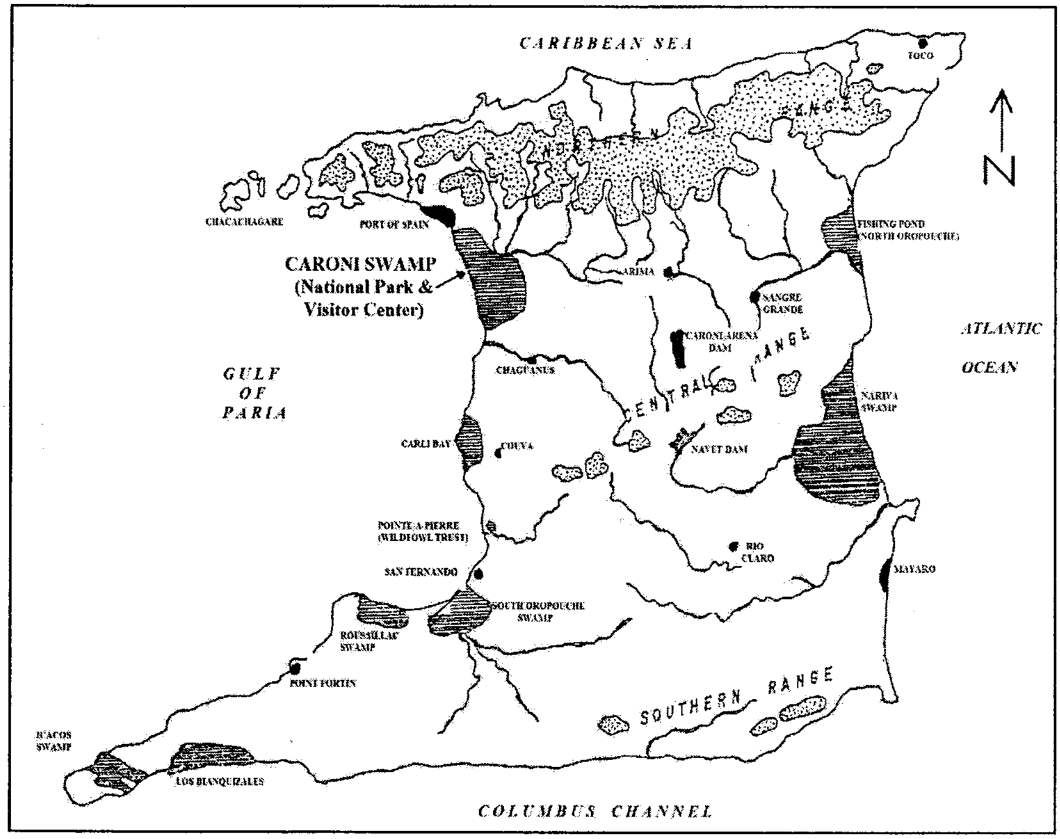
The diversity of flora and fauna in Trinidad and Tobago is due to its historical link to mainland Venezuela, part of the biogeographical region that includes the South America, Central America, the insular Caribbean and a large part of Mexico. Swamp and marshes are rare to this region, but abundant in Trinidad and Tobago, which therefore has unusual faunal and floral diversity (Bissessar 1999): approximately 2,610 plant species occur in the archipelago, of which 110 are endemic; 108 species of mammals, 420 species of birds (131 resident and 289 migratory), 93 species of reptiles, 34 species of amphibians, 24 species of fishes and 36 species of corals also occur. Trinidad's unique geographic location, which links the continental Neotropics and oceanic Antilles, places the island in a strategic position, being a major flyway between North and South America. Wetland areas provide ideal stop-over feeding and resting habitats for many migrating waterbirds (Cuffy 1999).

THE CARONI SWAMP

The Caroni Swamp is the second largest wetland in Trinidad and covers an area of 5,996.3 hectares. It is situated on the west coast of the island (10^0 36' N, 61^0 28' W), about 3.5 km southeast of the capital of Port-of-Spain (Figure 1.2) It is an estuarine system, comprising mangrove forest and herbaceous marsh, which is interlinked with numerous channels and brackish and saline lagoons with an extensive intertidal mudflat on the seaward side (Gyan and Juman 2005). The swamp is bordered on the north by the Caroni River, on the south by the Madame Espagnol River (also called the Cacandee River), on the east by the Uriah Butler Highway and on the west by the Gulf of Paria (Bildstein 1990).

Mangroves grow into independent clusters that form little islands completely surrounded by water. These islands serve as ideal nesting and roosting sites for many species of birds. The main mangrove species are red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia germinans*) and white mangrove (*Laguncularia racemosa*).

Figure 1.2 Map showing the location of the Caroni Swamp, other major wetlands and main towns in Trinidad, West Indies.



the red mangrove spreads rapidly and is considered a pioneer species in the internal lagoons. Red mangrove is important in the protection of erosion of forest on the Gulf of Paria (Bacon 1968). Black mangroves are not dominant, but form woodland and basin communities. White mangroves are fairly common in mixed basin forests, but do not form pure stands (Gyan and Juman 2005).

The fauna of the Caroni Swamp is very diverse in comparison to its flora. A total of 189 species of birds has been recorded in the Caroni Swamp (Cuffy 1999). This list includes resident, nesting water birds and migratory species, together with several species of forest and pasture birds that roost in mangroves. Over 18 species of wading birds (Ciconiiformes) have been recorded (ffrench 1991), of which the most prominent is the Scarlet Ibis because of its significance to the country's ecotourism industry. This species has not been reported to breed in any other wetland areas of Trinidad or Tobago. Other fauna of economic importance are the mangrove oysters (*Crassostrea rhizophorae*), mussels (*Mytella guyanensis* and *M. falcate*), "Callalou crab" (*Ucides cordatus*), and black conch (*Melongene melongena*).

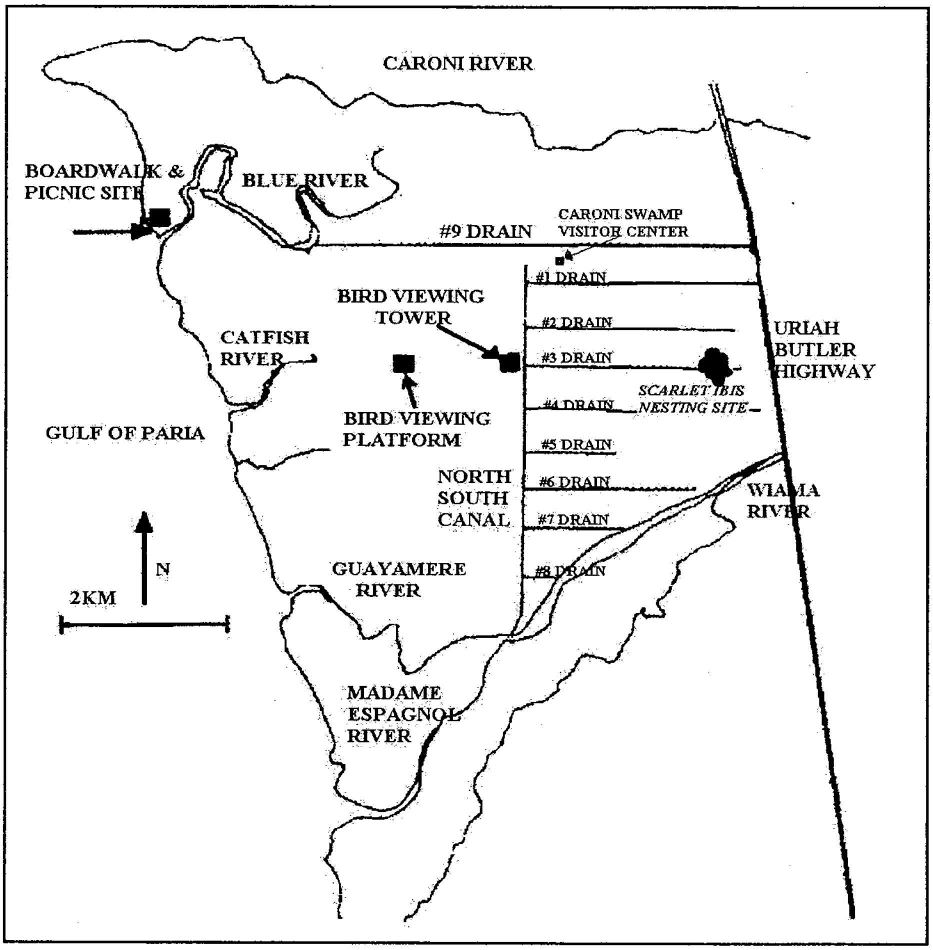
The Caroni Swamp is located in the Caroni River Basin hydrometric area, which covers approximately 22% of the island land surface (Gyan and Juman 2005). This swamp, under natural conditions, receives sediment laden freshwater inflow and overflows from the Caroni River and other adjoining rivers to the south. However, this natural drainage pattern was modified in 1921-1922 in an attempt to facilitate rice cultivation (Bildstein 1990). Nine channels were cut through the swamp in an attempt to drain areas. The attempt to establish long-term rice cultivation failed, but created a saltwater intrusion into the swamp. Aerial photos show the expansion of plants adapted to brackish water into the formerly freshwater swamp. These saltwater intrusions were further exacerbated by the construction of the Uriah Butler Highway and the channelization and diking of the Caroni River in the 1970s. These activities prevented the natural mixing and flow of fresh water during the rainy season and also reduced the nutrient input and normal sedimentation processes (Bildstein 1990). Such modifications to natural habitats have been suggested as possible causes for a lack of nesting activity in the Scarlet Ibis, but none of these issues has been directly linked to the reduction and eventual demise of breeding activities in the Caroni Swamp (Bildstein 1990).

The Caroni Swamp is easily accessible due to its central location in Trinidad. As a result, many surrounding villages have become dependent on the swamp as a supply of resources. Resource extraction activities, such as harvesting of red mangroves for leather tanning and construction of fishing pots, for fuel, for piling and for boat building were once regularly undertaken, some at unsustainable levels (Bacon 1968). As a result of the resource extraction and the increasing interest in the tourism potential of the Scarlet Ibis, concerns have arisen about depletion of the flora and fauna and pollution of the swamp. Consequently, the government designated the area as a Wildlife Sanctuary, initially for the protection of the Scarlet Ibis. During the period 1936 to 1960 several roosting and nesting sites of the Scarlet Ibis were declared as a Forest Reserve. In 1966, these sites, together with the areas surrounding them, were declared a Wildlife Sanctuary, and in 1979, the entire swamp was declared a National Park. However, in 1987, the main nesting areas for the Scarlet Ibis, located on the southern side of the No. 9 Drain, were declared a "Prohibited area", which means access to this area has been limited with a permit system issued by the relevant authority (Bildstein 1990) (Figure 1.3).

THE SCARLET IBIS (*EUDOCIMUS RUBER*)

The Scarlet Ibis is a highly social and active colonial nesting wading bird, named for its brilliant scarlet color (Elbin and Lyles 1993). It was previously assigned to the order Ciconiiforms, which comprises long-legged wading birds, including storks, herons and bitterns. However, ibises actually belong to the order Pelecaniformes and family Threskiornithidae, which includes 36 species of large terrestrial and wading birds. The family is further subdivided into two subfamilies: Ibises (Threskiornithinae) and Spoonbills (Plateinae) (Hackett *et al.* 2008). The Ibises are characterized by their long downward curved bills (Figure 1.4). They usually feed in groups probing in mudflats

Figure 1.3 Outline map of the Caroni Swamp, showing the boundaries and key features



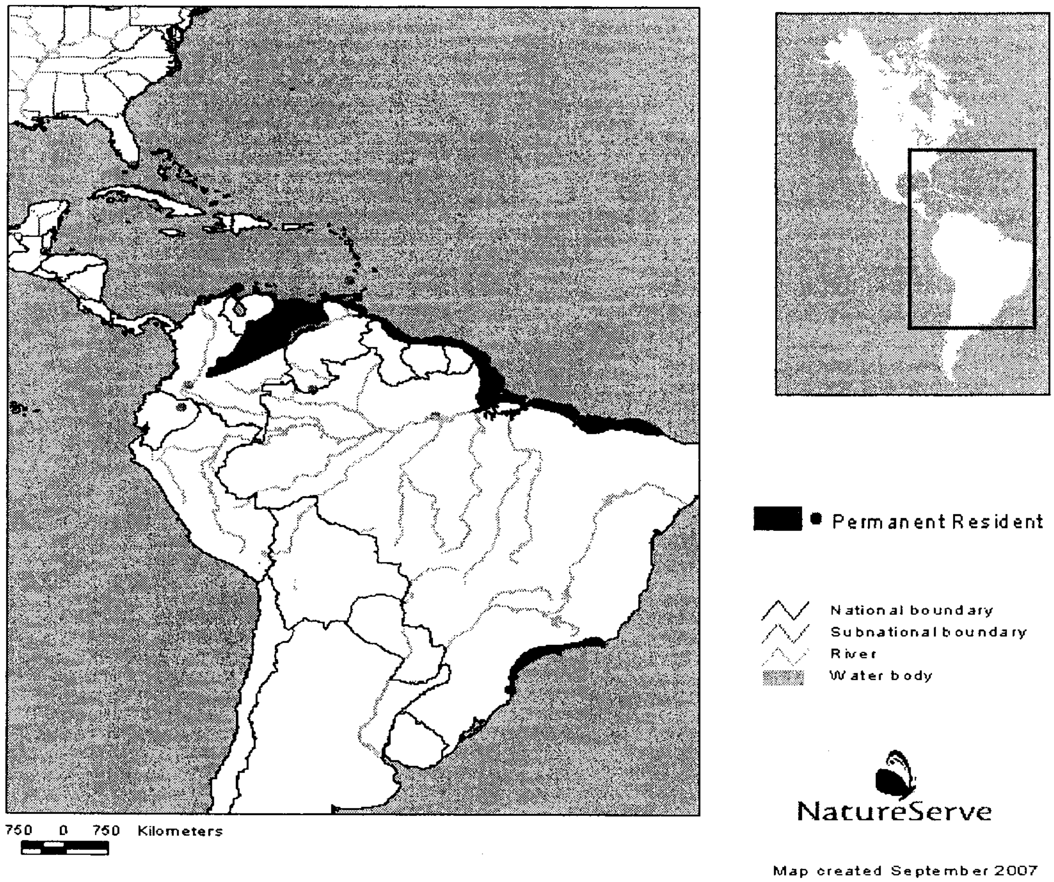
and other similar areas searching for crustaceans. There are 29 species of ibises which range throughout the world. Most species nest in trees with other birds, such as herons and spoonbills.

The Scarlet Ibis is a neotropical bird and is found throughout the northeastern coast of South America, from Colombia to Brazil. This area includes the Orinoco Llanos, Venezuela, Guyana, Surinam, French Guyana and Trinidad (Bildstein 1990) (Figure 1.4). Because of the similarity between the Scarlet Ibis to the White Ibis

Figure 1.4 The Scarlet Ibis (*Eudocimus ruber*)

(*Eudocimus albus*), their largely separate distributional ranges and evidence of mixed pairs copulations, it has been suggested that the ibises are in fact the same species, composed of two subspecies: *Eudocimus ruber ruber* and *Eudocimus ruber albus* (Ramo and Busto. 1987). The Scarlet Ibis is classified as a species of least concern on the World Conservation Union (IUCN) red list; this category indicates that the species has not declined in numbers more than 30% in the last 10 years or three generations. Under the Convention in Trade in Endangered Species of Flora and Fauna (CITES), the Scarlet Ibis is classified as an Appendix II species,

Figure 1.4 Maps showing the distribution of Scarlet Ibis



meaning that the species is not necessarily threatened with extinction, but may become so, unless trade in specimens of this species is subject to strict regulation in order to avoid utilization incompatible with their survival (Convention on International Trade in Endangered Species of Wild Fauna and Flora 2009). In Trinidad and Tobago the Scarlet Ibis is classified as a protected species and is on the prohibited list of animals that cannot be hunted (Conservation of Wildlife Act Chapter 67:01, Act 49 of 1963). This classification is due to the fact that the Scarlet Ibis is one of the national birds of Trinidad and is of significant eco- tourism importance for the Republic of Trinidad and Tobago.

Scarlet Ibises are highly colonial and their colonies usually consist of breeding aggregations that nest close to each other. It is suggested that the Scarlet Ibis initiates breeding at the onset of the rainy season (ffrench and Haverschmidt 1970). In Trinidad, this period usually begins during the middle of April or May. However, ffrench and Haverschmidt (1970) concluded, based on the data collected in the 1960s, that the Scarlet Ibis maintained a loose temporal breeding cycle, which was not triggered by climatic changes. They suggested that factors such as human disturbance, pollution from surrounding factories that dumped poisonous effluent into the swamp, and competition from other birds in the rookery such as Cattle Egrets (*Babulcus ibis*), Snowy Egrets (*Egretta thula*), Little Blue Herons (*Egretta caerulea*) and Night Herons (*Nycticorax* spp), may alter or inhibit the beginning of the breeding period for the Scarlet Ibis. In Southern Brazil, Olmos *et al.* (2001) reported that the Scarlet Ibis initiated its breeding during the second week of September, at the onset of the rainy season.

THE RATIONALE FOR THE WORK

The Scarlet Ibis, which was extirpated from Trinidad in the 1970s, but resumed breeding activity in the 1990s is faced with many problems. The bird's meat is considered a delicacy and its feathers were prized for the making of carnival costumes. Poaching occurs as a result. The Caroni Swamp is the final destination for the Caroni River, which traverses heavily populated and industrial areas and introduces high levels of pollution into the Scarlet Ibis habitat. For instance, Klekowski *et al.* (1999) found unusually high incidence of mutation in red mangrove in the Caroni swamp and high concentrations of mercury in the molted feathers of the Scarlet Ibis. Also, the Caroni Swamp is constantly under pressure from land reclamation, site manipulation and hydrological changes. The Caroni Swamp is below the direct flight path of approaching aircraft destined for the country's international airport. Together with these pressures, the Scarlet Ibis is also faced with the daily presence of tourist at their roosting site, coupled with the constant disturbance caused by people from the surrounding villages that use the Caroni Swamp for recreation and as a means of maintaining their livelihood through the process of harvesting of oysters, crabs and fish.

Despite the numerous problems faced by the Scarlet Ibis and its social and economic importance to Trinidad and Tobago, there is very little current information and research with regards to the present status, biology and behavior of the Caroni Swamp population to promote the successful management of this species. There are only two published studies for Trinidad and Tobago, one by ffrench and Haverschmidt (1970) on the Scarlet Ibis in Surinam and Trinidad, and the second by Bildstein (1990) on the status, conservation and management of the Scarlet Ibis. Unfortunately, these studies are over 38 and 17 years old respectively.

Based on historical records, the Scarlet Ibis has been recorded in the Caroni Swamp since the latter part of the 18^{th} century (Bildstein 1990; ffrench 1984). During the 1950s to the mid 1970s, the population fluctuated between 300 to 6000 birds (ffrench and Haverschmidt 1970a), and grew in excess of 10,000 by 1990 (Forestry Division 1992). Tour boat operators, who conduct tours to view the Scarlet Ibis coming in to roost at the Caroni Swamp, have estimated that there were about 8,000 to 12,000 birds (Personnal communication to D. Samayah, June 2008). In the last few years, however, and based on observations during the process of this research and bird counts conducted by the Forestry Division, this figure seems unrealistic.

Based on the work conducted by ffrench and Haverschmidt (1970), the Scarlet Ibis bred in the Caroni Swamp during the period 1954 – 1969, except for the years of 1964 and 1968. Since that time, some of the population has probably migrated to breed at Cotorra Island in Venezuela, but still continues to forage in the Caroni Swamp (ffrench 1984). Bildstein (1990) stated that breeding activities of the Scarlet Ibis completely ceased in the Caroni Swamp by the early 1970s, but that the birds continued to feed and roost within and around the Caroni Swamp during the non-breeding period. This cessation of breeding activities at Caroni Swamp has been attributed to the ecological changes that resulted from the alteration of water courses, for example inward movement of salt water into previously freshwater habitats, hunting and poaching activities, and the over-exploitation and mismanagement of the Caroni Swamp by its direct users, mainly tourists (Bildstein 1990). However, visual observations of new breeding activities were recorded by officers of the Wildlife Section of the Forestry Division in 1995 (Samayah *et al.* 1990).

Given the importance of the Scarlet Ibis to the economy and culture of Trinidad and Tobago, and the ongoing issue of increased human disturbance caused by tourism activities, the purpose of this thesis is to address two issues. First, from an ecological perspective, how is the breeding success of colonial waterbirds affected by human disturbance and do the effects of human disturbance on the breeding success, abundance and diversity of colonial waterbirds differ with biome, migratory habit and functional group, since factors such as migratory habits and functional grouping may influence their evolutionary and behavioral habits? Second, are laying and hatching success of the Scarlet Ibis in the Caroni Swamp related to factors such as height of the nests from the water, size of nesting trees, distance of neighboring nests, the number of nests per tree, the level of canopy cover and the location of the nest with respect to distance from the water. To address these two aspects, this research did the following:

1) Conducted a comprehensive literature review to determine how the effects of human disturbance on the breeding success, abundance and diversity of colonial waterbirds differ with biome, migratory habit and functional group.

2) Documented the nesting dynamics of the Scarlet Ibis at the Caroni Swamp, in Trinidad, West Indies during the 2008 breeding season, in an attempt to determine whether key parameters can influence the level of their reproductive success, and compare these parameters dynamics of the nesting site at the Caroni Swamp during the 2008 breeding season with that of other neotropical Scarlet Ibis populations as reported in the literature.

In Chapter I, this paper has aimed to provide general information that forms the foundation of this thesis. The objective of this section has been to orient readers and serve to reinforce the relevance of this study and its importance to Trinidad and Tobago.

A second chapter provides a review of the literature on human disturbance of colonial waterbirds. It compares the effects of human disturbance on breeding success, abundance and diversity of colonial waterbirds with respect to biome (whether a population occurs in a tropical or a temperate area), migratory habit (whether a migratory species or resident species is being considered), and functional group (whether waders or seabirds are being considered). These factors were chosen because they affect the feeding efficiency, feeding rate, diversity, abundance, adaptive nature, ability to habituate, ability to store food and many other functions of colonial waterbirds (Kenyon; 2005; Brawn *et al.* 2001; Nisbet 2000; Carney and Sydeman 1999).

Chapter 3 reports on data collected for the Scarlet Ibis during the 2008 nesting and breeding activities in the Caroni Swamp, Trinidad. Its aim is to determine if the breeding and nesting success of the Scarlet Ibis is attributed to the characteristics of nesting sites, in particular spatial structure. In chapter 4, the work is summarized to integrate the results of chapter 2 and 3, provide management implications and identify future research.

CHAPTER 2, THE EFFECTS OF HUMAN DISTURBANCE ON BEHAVIOUR AND ABUNDANCE OF COLONIAL WATERBIRDS: A REVIEW.

INTRODUCTION

The effects of human disturbance on colonial waterbirds are a major focal point for research among wildlife biologists. Ecological and economic implications associated with the subject include the potential for colonial waterbirds to generate revenue and create employment via sustainable ecotourism (Lim and McAleer 2005; Naidoo and Adamowicz 2005; Uyarra *et al.* 2005). Birds are also considered important environmental indicators that identify habitats such as foraging and nesting areas, while serving as sentinels of environmental health and changes that are evident by changes in their behavior and abundance (Birdlife International 2004; Carson 1962). They also help in linking cultures and serving as a focal point for local and international conservation efforts (Kirby *et al.* 2008). The role of birds as environmental indicators is likely to increase in importance due to population growth, global warming, pollution, and alien invasive species. These factors, in addition to the potential for overexploitation of colonial birds by ecotourism and recreation, are serious treats to species survival, diversity and site and habitat quality (Birdlife International 2004). Habitat destruction and degradation includes losses to rainforest, swamp forest and dry forest (Sodhi and Smith 2007). The largest areas of mangrove swamps occur in Asia and the Americas (Louisiana in the USA and the Brazilian Amazon) and at least 35% have been lost during the past two decades. Losses to swamp forest are an especially important issue, because such wetlands serve as important areas for migratory stopovers and for resident birds (Valiela *et al.* 2001).

Colonial waterbirds, typically occupying forest swamps are considered one of the most fascinating groups of birds by biologists and observers alike. They are characterized by their large aggregations and feeding habits, in which they obtain most or all of their food from the water (Yorio *et al.* 2001; Burger 1998). Examples include the Scarlet Ibis (*Eudocimus ruber*) in Trinidad, West Indies (Bildstein 1990; ffrench 1987), American Flamingos (*Phoenicopterus ruber ruber*) in the Yucatan, Mexico (Galicia and Baldassarre 1997), or Common Terns (*Sterna hirundo*) in Barnegat Bay, New Jersey (Burger 1998).

Avian aggregations often attract visitors from all parts of the world and have also fueled a new ecotourism industry. However, human activities such as ecotourism and recreation can have a direct and significant effect on colonial waterbird species behavior and abundance (Carney and Sydeman 1999). Repeated intrusion has the potential to cause impacts that accumulate through time and are manifested as progressive declines in avian richness and abundance (Riffell *et al.* 1996). Ecotourism involves activities such as nature-watching, bird-viewing or travel to new places. According to the United Nations World Tourism Organization (UNWTO), there were over 903 million international tourist trips in 2007 (a 6.6% increase over 2006), which accounted for $856 billion US-D in tourist expenditure (United Nations 2009). Recreation, which can involve consumptive forms such as hunting and fishing or non-consumptive forms such as outdoor leisure activities, for example cycling, jogging, hiking, kayaking and boating, is the other major form of intrusion (Blanc *et al.* 2006; Boyle and Samson 1985).

Mitigating human disturbance, while taking advantage of the economic potential afforded by colonial waterbirds, is considered a serious management dilemma. On one hand, exploitation of an area for human use can create revenue and generate conservation strategies; on the other hand, human disturbance can cause a population to abandon a critical nesting or roosting site (Carney and Sydeman 1999). This predicament has led to several reviews on this issue of the impacts of human disturbance on colonial waterbirds, each focusing on specific aspects. For instance, Carney and Sydeman (1999), Nisbitt (2000) and Korschgen and Dahlgren (1992) looked at the issue holistically, while Boyle and Samson (1985) and Blanc *et al.* (2006) considered it from the standpoint of limited non-consumptives activities, and Tamisier *et al.* (2003) and Thiel *et al.* (2007) examined the impact of consumptive activities. Some reviewers, such as Miller *et al.* (2001; 1998) considered the impact of human disturbance from the perspective of the species response. These reviews focused on factors such as breeding success, behavioral changes and feeding efficiency in colonial waterbirds with respect to human disturbance. However, the concept of looking at these effects over different ranges, or based on inherent habits of a species to migrate, as well as based on their classification in the global perspective has never been reviewed. Such classifications are important, because colonial waterbirds differ based on the habitat that they utilize, due to different levels of resources and their seasonal habits which would determine their feeding efficiency and energy requirement, as well as their functional grouping which can influence their choice of habitat selection and adaptation, and their habituation to human disturbance. The purpose of this paper is to classify colonial waterbirds based on their biome, temperate or tropical, their habit, migratory or resident, and their functional group, waders or seabirds, and to determine whether the impact of human disturbance such as habitat destruction or manipulation, competition for resources, exploitation of resources and general disturbance, is globally similar or whether it differs across these parameters. This paper first discusses the overall concept of human disturbance and some of the conflict that arises from ecotourism and recreational activities in areas of colonial waterbirds, and then address various forms of human disturbances, and look at their general effects on critical attributes of colonial waterbirds (breeding success and/or other features), and how these effects may differ with biome, habit and functional groups, this review will categorize and discuss some factors that may have an influence on the extent of the effect of human disturbance. Finally, the assessment of colonial waterbirds based on biome, habit, and functional grouping will be discussed with regard to management objectives and implications for future research into their reproductive success, and physiological behavior.

HUMAN DISTURBANCE

Boyle and Samson (1985) suggested that the concept of disturbance might be very confusing because of its general association with perturbation, that is, with discrete events such as storms or droughts, as well as with human influenced activities that may affect populations, ecosystems or landscapes. Nisbet (2000) defined human disturbance as “any human activities that changes the contemporaneous behavior or physiology of one or more individuals within a breeding colony of waterbirds.” This definition is best suited to this review, because it can take into account two key components: human activity and behavioral or physiological attributes of the bird. The action of humans or human disturbance may be the driving factor that leads to changes or impacts in the behavior and physiology of the birds. For example, Galicia and Baldassarre (1997) showed that human disturbance directly increased alert behavior by 400% and reduced feeding time by 40% in non-breeding Flamingos, but that the birds resumed feeding within 20 minutes after the disturbance caused by tour boats ended.

The last example is typical of contemporaneous changes to behavior. However, disturbances can create several different behaviors that are not typical with colonial waterbirds daily habits, therefore, it is more important to look at behavioral changes more holistic or from an ethological perspective. Also, such ethological changes do eventually lead to changes in distribution and abundance, and this can best be classified as ecological changes and should be included in a definition. Therefore, this review defines human disturbance as "any human activities that change the contemporaneous physiological and ethological (behavioral) state of any individual bird or group of birds, thereby affecting its ecological balance". This definition is more general and encompasses a holistic approach to the effects of human disturbance on birds.

METHOD

Literature for this review was sourced from Web of Science, JSTOR article databases and Google Scholar internet search engine. Article searches were conducted using the following headings: birds, waterbirds, colonial waterbirds, disturbance, human disturbance, human influence, species diversity and species abundance. Articles were selected based on their relevance to the topic of human disturbance, with special emphasis on ecotourism and recreational activities. Because of the quantity of studies on human disturbance and colonial waterbirds, only articles published during the period 1990 to 2008 were reviewed. Articles were evaluated based on their classification according to biome, habit and functional group of waterbirds, and based on the type of disturbance investigated and the individual and population level responses reported; however there was much overlap with respect to these classifications.

Biome – Temperate and Tropical Species

According to Koeppen's (1918) Climate Classification, there are five major climate types based on the annual and monthly averages of temperature and precipitation. They include Moist Tropical Climates, Dry Climates, Humid Middle Latitude Climates, Continental Climates and Cold Climates. These five major climate types can be further condensed into three basic climate groups that show the dominance of air-mass sources. Group I is Low-Latitude Climates, which include Tropical Moist Climates, such as rainforest, Wet-Dry Tropical Climates such as savanna, and Dry Tropical Climates, like desert. Group II is Mid-Latitude Climates, comprising Dry Mid-Latitude Climates, such as steppe and grasslands, Mediterranean Climates, such as chaparrals (wet winter, dry summer climate), and Moist Continental Climates, such as deciduous forests. Group III is High- Latitude climates, including boreal forest and tundra (Muller and Oberlander 1978; Strahler and Strahler 1979). For the purpose of this review, temperate waterbird species will include those that can be found in climates corresponding to Groups II and III, and tropical species will be considered those in Group I.

Biome is an important classification in understanding the effects of human disturbance on colonial waterbirds because approximately 74% of bird species can be found in tropical and sub-tropical regions (Birdlife International 2004). These regions provide adequate primary and secondary feeding ground for many resident and migratory species. However, the availability of similar foraging and nesting habitats in temperate regions may be limited due to extremes in weather conditions during the winter season. Therefore, birds in such biomes must take advantage of favorable weather conditions for key processes such as breeding and energetic gain. The small window of opportunity may make colonial waterbirds in temperate regions more vulnerable to human disturbance.

Habit: Migratory and Resident Species

The abundance and diversity of colonial waterbirds may be dependent on the inherent habits of migratory or residential species. Bird migration is the process by which birds move seasonally from one area to another as a result of food availability, habitat or weather conditions. The Convention on the Conservation of Migratory Species of Wild Animals (CMS) defines a migratory species when "the entire population or any geographically separated part of a population cyclically and predictably crosses one or more national jurisdictional boundaries." (United Nations Environmental Programme 2009). According to Kirby *et al.* (2008), the strategy of migration has fascinated mankind, and there are many benefits that can be derived from studying migratory birds, such as the linking of human cultures and development, the creation of international collaboration, and initiation of international conservation measures. Migration strategies vary across species, ranging from short, inter-regional movement to intercontinental flight. The distance that birds travel during migration also varies. These variations in strategy pose serious implications for conservation, because human disturbance may differ at the various stop-over sites (Kirby *et al.* 2008).

Resident species do not make any seasonal movement to other locations. Birdlife International defines resident birds as those that are known or thought to be resident to a country (although some resident birds that move within the United States of Americas are considered migrants), and migrants as those that visit regularly during the breeding season. Although resident birds are equally susceptible to human disturbance, migratory species have a tendency to be more sensitive to human disturbance than resident species (Klein *et al.* 1995). For example, Klein *et al.* (1995) found that some migratory ducks were most sensitive to human disturbance, while other species of colonial waterbirds such as herons, egrets, Brown Pelicans (*Pelicanus occidentalis*) and Anhinga (*Anhinga anhinga*) showed greater tolerance to human activities at one site. Such tolerance could be attributed to habituation of a species to human disturbance.

Functional Group – Seabirds and Waders

The term waterbirds refers to a large functional group of birds that includes several different classifications. Field terms such as migratory birds (Kirby *et al.* 2008; Quan *et al.* 2002), shorebirds (Rogers *et al.* 2006; Yasue 2005), wading birds (Peters and Otis 2006; West and Caldow 2006), staging birds (Laursen *et al.* 2005; Bechet *et al.* 2004), coastal birds and waterfowl (Norris *et al.* 2004; Mori *et al.* 2001) were frequently used in the literature reviewed. However, for the purpose of this review, colonial waterbirds will be classified following the U.S Fish and Wildlife Service, Division of Migratory Birds (US Fish and Wildlife Service 2001). Under this classification, colonial waterbirds is the collective term for a large variety of different species that share two common characteristics: (1) they tend to gather in large assemblages during the nesting season and (2) they obtain most or all of their food from the water. Colonial waterbirds are sub-divided into two functional groups. The first are seabirds, which feed primarily in saltwater. However, a few members of this group, such as cormorants, gulls and terns, also occupy freshwater habitats. Some spend almost their entire lives at sea, returning to land only to nest, while others are confined to narrow coastal interface between land and sea. The second functional group is waders. These birds feed primarily in fresh or brackish waters, mainly by wading or standing still in the water waiting for prey to swim within striking distance. The group includes bitterns, herons, egrets, ibises, spoonbills and storks. Waders' are however referred to as shorebirds in North America, so throughout this review they may be used interchangeably.

Seabirds and waders depend on different environments for the acquisition of food, roosting and nesting; it is likely that the impacts of human disturbance will vary between these classes. For instance, due to the inherent cost of visiting seabirds and conducting research at remote locations, less human disturbance is likely to occur for this functional group. On the other hand, in many coastal and wetland ecosystems, waders like seabirds are considered top consumers (Burger 1990), and issues such as human impact on their food supply can easily influence this functional group. Other issues that are of importance to both functional groups are sustainable yield for hunted species, non-consumptive use of fragile habitats, climate change and rising sea levels (Burger 1990).

SOME ASPECTS OF COLONIAL WATERBIRDS THAT MAY INFLUENCE HUMAN DISTURBANCE

The study of human disturbance and its effects lacks any standardized and uniform body of terminology, evident by the ambiguity and inconsistent terms used in the literature (Taylor and Knight 2003). For example, Ellenberg *et al.* (2006) concluded that animals may react to human disturbance without showing any "physical signs" such as movement, while Baudains and Lloyd (2007), suggested that the overall "reproductive fitness" of wild birds may not always be compromised by human disturbance and urbanization, and Olmos (2003) suggested that the colonial behavior of waterbirds has been considered as a strategy for "reducing predation, finding ample food supplies and sexual and habitat selection". These are just examples to demonstrate the amount of ambiguity presented in the literature with respect to the actual responses studied by several researchers. Therefore, it is imperative to have a definitive vocabulary in the field of human disturbance research. Behavioral responses could be categorized in to three broad groups; ethological effects, which could include the general behavior of the animal, physiological effects, such as on reproduction, breeding, nesting and mate acquisition, and ecological effects, which could entail effects on distribution and abundance.

Ethological Effects

Understanding effects of human disturbance on colonial waterbirds involves the study of the animal behavior, that is, an animal's action or reaction to people. Interpretation of these actions can differ. The deviation in a bird's action from its habitual norms based on changes in their environment caused by human or natural phenomenon can be considered as an ethological response, because the disturbance elicits some sort of response or movement that is contrary to their normal reaction. However, based on individual perspective or their attempt to produce new and revealing research, researchers have referred to similar ethological responses by different titles. For example, the practice of stopping feeding activities and looking around has been measured as scanning rate (Frid and Dill 2002; Galicia and Baldassarre 1997), vigilance rate (Fernandez-Juricic *et al.* 2007; Devereux *et al.* 2006; Walker *et al.* 2006), flight initiation distance (Runyan and Blumstein 2004; Blumstein 2003) and alert distance (Blumstein 2003; Taylor and Knight 2003; Fernandez-Juricic *et al.* 2001). Similarly, the distance a bird moves when it is disturbed, has been referred to as distanced moved (Taylor and Knight 2003; Miller *et al.* 2001), flushing distance (Mori *et al.* 2001), and escape distance (Burger *et al.* 2007; Laursen *et al.* 2005). Such variation in the definition and measurement of these behaviors may be due to the simplicity of observing these actions, or the narrow distinction between one action and the next.

Physiological Effects

Physiological effects may be more difficult to determine than ethological effects, because changes in physiology must refer to a definitive aspect of the birds' life cycle, usually the reproductive and breeding period. During this stage of the birds' life cycle they are very reclusive and tend to construct their nest in very well camouflaged areas. During the breeding season, the most common physiological effects that are measured are breeding behavior, reproductive or breeding success, mate acquisition and parental investment. For instance, the breeding success of Brown-headed Cowbirds was studied to determine the effects of hiking trails proximity on the selection of site for nesting (Miller *et al.* 1998), and similar work was also conducted by(Yasue and Dearden 2006) on the Malaysian Plover to determine the impact of tourism development on their habitat availability and reproductive productivity. Whereas these researchers looked at reproductive success and nesting site selection, Müllner (2004) went deeper by looking at plasma concentrations of corticosterone (stress hormone), to investigate if young Hoatzins were physiologically stressed by tourism activities. Walker *et al.* (2006) also used this approach on Magellanic Penguins.

Ecological Effects

Effects of human disturbance on ecology include effects on the distribution and abundance of an individual or species throughout its range. This range may vary from a small lake to areas that cross international boundaries that serve as flyways or stop-over sites (Kirby *et al.* 2008). A reduction in species richness and distribution has been associated with native population declines due to decreased breeding success, changes in foraging sites, and diminished feeding rates. The fleeing and replacement of resident species by more prolific and adaptive species, that are able to habituate quickly to human activities is another factor that contributes to reduction in species richness and distribution (Cardoni *et al.* 2008). This statement probably explains why the most common ecological issues that are measured with respect to the effect of human disturbance on colonial waterbirds are distribution, species richness, abundance and density and displacement.

HUMAN DISTURBANCE ON COLONIAL WATERBIRDS: BIOME, HABIT AND FUNCTIONAL GROUP

Waterbirds respond differently to disturbance based on their body size (Blumstein *et al.* 2005), fitness level (Rogers *et al.* 2006; Bechet *et al.* 2004), distance to neighbors and flock size (Fernandez-Juricic *et al.* 2007), availability of food (Yasue 2005; Gill *et al.* 1996) and several other factors. Therefore, in order to make effective management decisions that can be applicable to birds across different biomes, with different movement habits, and which belong to different functional groups, managers must have a clear understanding of how these various factors relate to each category.

It was difficult to derive clear and precise distinctions across these categories from the literature reviewed. In summary, there were more than twice the number of studies conducted in temperate regions compared to tropical regions, and most of these were done in the Florida, U.S.A. area, with a few in Malaysia and Thailand. For the tropical regions, study mainly focused on general breeding and foraging behavior of specific waterbird species, with little or no study found pertaining to the effects of human disturbance (Martinez 2004; Olmos and Silva 2001; Frederick and Bildstein 1992). There was an almost equal amount of literature involving resident species and migratory species. With respect to functional group, there were almost twice the numbers of articles on wading species and human disturbance compared to articles on seabirds and human disturbance.

Effect of Human Disturbance Across Biome

The effect of human disturbance across biomes appears similar. In terms of ethological studies based on biome, the main behavioral characteristic that was assessed was foraging behavior, which usually included prey selection and searching (Yasue 2006; Madsen 1998; Gill *et al.* 1996), escape distance (Laursen *et al.* 2005; Erwin 1989; Vos *et al.* 1985) and flight behavior (Martinez-Abrain *et al.* 2008; Mori *et al.* 2001; Burger 1998; Erwin 1989). In research in a temperate region, Yasue (2005) showed that the impact of human disturbance on feeding rate was not affected by flock size. But, Mori *et al.* (2001) found that flock size positively influences the distances birds fly (escape distance) after a disturbance event, and that this escape distance may not be the same for all species in different areas (Laursen *et al.* 2005). Fitzpatrick and Bouchez (1998) also found that human disturbance did not reduce the food searching ability or efforts over different species in temperate regions, but actually caused birds to increase their prey capture rates, due to limited disturbance-free time. On the other hand, Martinez-Abrain *et al.*(2008) found that Yellow-legged Gull (*Larus michahellis*) in the tropic tend to habituate to large human presence but still kept their antipredatory mechanism, and larger dense groups were more reluctant to fly away from disturbance than smaller groups.

Physiological variations in response to disturbance for tropical and temperate waterbirds appear not to differ much also. The main physiological characteristics that have been studied are breeding success and nesting success, both by means of general observation and by testing stress hormones (Ellenberg *et al.* (2006). In tropical regions, Mullner *et al.* (2007) reported similar nesting and hatching success in disturbed and undisturbed sites visited by tourists however, chick survival was much lower at disturbed sites. In another tropical region, Baudains and Lloyd (2007) reported that daytime nest attentiveness decreased with increasing experimental disturbance at two sites experiencing different levels of human disturbance, and for any given level of disturbance, incubating birds at the more disturbed site had lesser nest attentiveness. Changes in the selection of breeding sites and nest desertion with human disturbance has also been documented for tropical species such as the Malaysian Plover (Yasue and Dearden 2006), and others have described the variation in physiological response to disturbance by species (Yorio *et al.* 2001; Erwin 1989), stage of breeding period (Yorio *et al.* 2001; Burger 1998; Vos *et al.* 1985) and colonial makeup (Erwin 1989). One example of sensitivity in birds caused by human disturbance was highlighted by Parsons and Burger (1982), nestling Black Crowned Night Herons (*Nycticorax nycticorax*) actually regurgitated their meal following human disturbance and failed to feed on it again, leading to reduction in body weight. However, although Yasué and Dearden (2006) reported some nest desertion, they also observed that fledgling success was not totally affected in the tropics by human disturbance for the Malaysian Plovers, which showed very little overt response to disturbance. In tropical biome, heat stress may be an overriding factor contributing to lower productivity and may mask the effect of human disturbance. Mullner *et al.* (2004) reported that hatchling survival in tropical regions was closely correlated with post-fledging losses because incubation and hatching success may not always be affected by any disturbance. In temperate regions, similar strategies to the Malaysian Plover were observed. Parsons and Burger (1982) found that nestling Black-crowned Night Heron habituated to investigators and that the weights of disturbed and undisturbed groups were similar. Erwin (1989) highlighted that there were few relationships between flushing distance and colony size and also few differences in response during the hatching and post-hatching period in various bird species in colonial coastal sites in Virginia, U.S.A. Vos *et al.* (1985) identified that 67% of all human disturbance caused no flushing response in herons in north central Colorado, and only 27% of human disturbance elicited any temporary nest abandonment. At more disturbed sites in the sandy coastlines along Cape Peninsula, South Africa, the White-fronted Plover (*Charadrius marginatus*) showed greater nest attentiveness and colonies also experienced significantly lower nest mortality from mammalian and corvid predators due to a high human presence, because mammalian and corvid predators such as crows, ravens, and other similar species tend to avoid areas with higher levels of human activity.

Common to both tropical and temperate studies, bird density will vary between sites (Lafferty 2001), and feeding sites with more food supply will maintain larger colonies (Gill *et al.* 2001; 1996). The level of disturbance caused to birds will vary depending on the intensity of the disturbance (Madsen 1998). In addition Rogers *et al.,* (2006) indicated that roost availability may be a more important factor in determining bird diversity than the effects of human disturbance.

Effects of Human Disturbance based on Bird Habit

Comparing the effects of human disturbance between resident and non-resident (migratory) species has never been the main focus of any study. Both resident and migratory birds are generally susceptible to the same ethological, physiological and ecological effects of disturbance, because they are similarly vulnerable to human disturbance, for example, changes in vegetative cover and reduction in beach width (Yasue and Dearden 2006). However, tropical species may be more at risk due to poor conservation regulations and unplanned local development on beaches. Birds may be forced to nest in higher densities, eventually leading to lower breeding success. For example, following reduction in habitat associated with human disturbance, adult Malaysian Plovers in Pachena Beach, British Columbia, Canada were forced to spend more time defending their nesting area, thereby leaving eggs and chicks more exposed to predators and heat stress.

Klein *et al.* (1995) highlighted that resident species may be less susceptible to disturbance than migratory species. Their study showed that migratory dabbling ducks were the most sensitive group of waterbirds to human visitation. When compared to resident species, such as the Snowy Egret (*Egretta thula*), migratory ducks tended to be more sensitive when they first arrived at a site, earlier in the season. Resident species also displayed two distinct types of behavior towards human disturbance; the first form of behavior involves habituation and the second sensitivity towards human disturbance. This behavior of habituation by resident species was mentioned by Mullner *et al.* (2004) who reported that adult Hoatzins (*Opisthocomus hoazin*), occupying lakes in the Amazonian rainforests showed greater tolerance of human presence when incubating. Flushing distance of habituated Hoatzins was 50% lower than for birds in undisturbed sites. Similar traits of habituation among resident species were identified by Burger and Gochfeld (1998). At Loxahatchee (Arthur B. Marshall National Wildlife Refuge), part of the Everglades, southern Florida, U.S.A., some species such as the Sora Rail (*Porzana carolina*) and the Gallinules (*Gallinula* spp), tended to habituate more quickly to human disturbance than other species such as the Little Blue Heron (*Egretta caerulea*) and the Tri-colour Heron (*Egretta tricolor*). This habituation behavior meant that resident species were able to spend more time feeding in the presence of people while other migratory species retreated.

Birds may change their response to human disturbance according to their individual state and the state of the environment in which they find themselves, regardless of the intensity of human disturbance (Beale and Monaghan 2004). Since it is generally understood that tropical feeding grounds provide richer and more abundant sources of food, resident tropical species should be more physically fit than migratory species. However, there are other factors that may affect physical fitness and reproductive productivity, such as inclement weather and predator abundance (Erwin 1989). Yasué and Dearden (2006) found that levels of predation increased with the presence of migratory predators such as falcons and Sparrow Hawks.

<u>Effects of Human Disturbance Based on Functional Groups</u>

As with biome and habit, the effects of human disturbance appear similar for seabirds and waders, but there are some acute differences. Common to both groups are increased vigilance and flight from foraging locations when human disturbance is introduced. However, Burger (1998) observed that the degree of sensitivity varied among seabird species, based on the type and intensity of the disturbance, for instance, common terns (*Sterna hirunto*) exhibited greater response to personal water crafts than motorized boat due to the high level of noise that they produce. Waterbirds also differ in body size and group composition and these factors may affect response to human disturbance. For example, in the Gulf of Thailand, the Malaysian Plover, which is a relatively small shorebird, rarely moved large distances when approached by people (Yasue 2006). On the other hand, Rodgers and Smith (1997) indicated that larger species of waders, such as the Tri-colour Heron and Great Egret (*Ardea alba*) in central Florida, U.S.A., often had longer flushing distances. Similar observations were made by Bechet *et al.* (2004), who found that birds such as Greater Snow Geese (*Anser caerulescens atlanticus*) flew longer distances after a disturbance event caused by humans, than after disturbance of a fortuitous nature, however, the distance flown usually decreased as flock size increased. Group influence was also confirmed by Mori *et al.* (2001), by comparing flight distances of waterbirds disturbed by boats. Flight distance was positively correlated to flock size of waders, such that Widgeons (*Anas penelope*), Spot-bill Ducks (*Anas poecilorhynchoa*), Green-winged Teals (*Anas crecca*) and Petards (*Aythya ferina*) had relatively short flight distances as individuals, but in groups, they had much longer flight distances. Birds that flew relatively long distances were not affected by flock characteristics. Greater flock size in waders resulted in lower feeding rates, likely due to the interference between flock members (Yasue 2005).

Human disturbance distracts waterbirds and reduces their ability to concentrate on capturing prey (Yasue 2005). However, some species of seabirds compensate by increasing feeding rates and extending feeding periods to late in the evening and very early in the morning, although this response tends to vary with prey abundance. Shorebirds such as Plovers and Sandpipers that fed in areas with high human disturbance or low prey density extended their feeding time during high tide and at night. These birds resumed feeding more quickly in areas with high prey availability or during late afternoon and responded less to human disturbance or natural disaster when there was a significant energetic or fitness cost involved (Yasue 2005).

One interesting example pertaining to shorebirds was the concept of "hyper sensitization," which implies that a species may react to some forms of human disturbance more quickly in some situations or from greater distances on days when the risk of getting disturbed is high, but that this variation does not occur for other forms of disturbance, such as the presence of dog. This hypersensitivity was observer in shorebirds such as Plovers and Sandpipers at a southern California beach, U.S.A., and was probably due to the fact that birds are constantly chased by dogs on the beaches (Peters and Otis 2006; Lafferty 2001). However, a similar behavioral response has not been reported for any of the seabird species. Peters and Otis (2006) suggested that bird response to human disturbance is most likely driven by a complex interaction of several factors such as weather, life history stage and resource availability. Extraneous factors such as tidal stage and wind conditions, affected the possible response of wading birds to disturbance in the creek at Cape Romain National Wildlife Refuge. McGowan *et al.* (2002) reported that the responsiveness of Red Knots to disturbance was affected by small changes in environmental conditions, such as wind speed and air temperature.

THE CONFLICT IN HUMAN DISTURBANCE RESEARCH

The concept of multiple effects of human disturbance on birds has spurred serious debate, in part because of conflicting views of researchers. Many have concluded that human disturbance always leads to negative impacts on birds. For example, Paillisson *et al.* (2002) reported that a ban on hunting in January 2000 at the Grand-Lieu Floodplain in western France contributed to a 55 to 65% increase in a duck population. At the same time, changes to the water management regime that resulted in a decrease in spring water levels from 1998 to 2000 were shown to reduce bird abundance Quan *et al.* (2002).

Other research suggests that human disturbance may not have had any impacts on certain birds, or may be beneficial to colonies, as birds might also habituate to human activities. For example, an examination of the endangered cavity nesting Stitch Bird or Hihi (*Notiomystis cincta*) by Lindsay *et al.* (2008) showed that there were no differences in the reproductive success or nesting site selection of birds that nest in areas close to public walking tracks compared to those in areas from which the public was restricted. Borghes (2008) showed that the number of edge species and non-forest species increased with human activities in Northern Kenya. Baudains and Lloyd (2007) discussed possible benefits of human disturbance to White-fronted Plovers for which they found that nest mortality due to natural mammalian and corvid predators was significantly lower at sites that experienced high recreational activities.

Nisbet (2000) implied that the study of the effects of human disturbance on colonial waterbirds is biased, due to the fact that many researchers only used data on the negative impacts of human on birds from their research. He also suggested that the concept of habituation is erroneous, and that in order to truly study this behavior, there must be rigorous documentation of longitudinal measurements of response in individuals subjected to controlled, repetitive forms of the same stimuli. Proof of habituation will require sequential measurements of tolerance within groups of individuals that are the same. However, habituation is a realistic and direct consequence of human disturbance. According to Walker *et al.* (2006) changes in the defensive, head turning actions of adult Magellanic Penguins (*Spheniscus magellanicus*) and their corticosterone levels showed that these animals habituated to human visitation quite rapidly. Baudains and Lloyd (2007), recorded similar behavioral adaptation in White-fronted Plovers, for which there was decreased daytime nesting attentiveness at both disturbed and undisturbed sites, allowing closer human approach, after which adults returned very quickly to the nest. Martínez-Abraín *et al.* (2008) concluded that ground nesting Yellow- legged Gulls (*Larus michahellis*) habituated to human presence, while retaining their antipredatory mechanisms.

There are several factors that influence the effect of human disturbance on colonial waterbirds. These factors range from physical attributes of the bird, such as body size, to environmental variables, such as food availability. For ease of discussion, these factors can best be classified as animal factors, disturbance factors and environmental factors.

Animal Factors and Human Disturbance

Each species of birds may respond differently to the disturbance caused by humans, with different consequences throughout its hierarchal ecological organization (Heil *et al.* 2007). Bratton (1990) studied boat disturbance of ciconiiformes in some Georgia, U.S.A. estuaries and found that Snowy Egrets were the least sensitive to boats, while Great Egrets (*Casmerodius albus*) and Great Blue Herons (*Florida caerula*) were more easily disturbed. In forested birds, generalist species such as Blue Jays (*Cyanocitta cristata*), American Robins (*Tardus migratorius*) and Brown-headed Cowbirds (*Molothrus ater*) are more abundant within the vicinity of recreational trails than specialist species (Miller *et al.* 1998). Burger *et al.* (2007) showed that Laughing Gulls

(*Larus atricilla*) returned to their pre-disturbed activity within 5 minutes of disturbance, whereas other species, such as waders, took much longer.

Variation in a species response to disturbance may be a factor of its body size (Laursen *et al.* 2005) or sex (Fernandez-Juricic *et al.* 2007; Thiel *et al.* 2007). Species with greater body sizes usually have a longer escape distance (shortest distance at which birds flush when a person or another disturbing stimuli approaches). The effect of human disturbance can differ between male and female birds. Female birds are usually the focal point for most research due to the nature of the research questions. Most research concerning the effect of human disturbance on colonial waterbirds is focused on definitive periods such as breeding and reproductive stages, and for many species, the males are absent at these times. Capercaillie (*Tetrao urogallus*) males flushed at consistently longer distances than females during hunting and other recreational activities such as jogging, due to their larger body size (Thiel *et al.* 2007). The impact of sex was also observed in Brown-headed Cowbirds, in which males were found to be more vigilant than females (Fernandez-Juricic *et al.* 2007). The size of groups associated with a bird population may influence the effect of human disturbance, because it is assumed that there is safety in numbers. Fernández-Juricic *et al.* (2007) discovered that group size and distance of neighbors affected foraging and vigilance rates of the Brown-headed Cowbirds, for which pecking rate, food-handling rate and duration of food-handling bouts changed significantly with flock size and distance of neighbors. Yellow-legged Gulls also showed similar traits in large groups, when they were more reluctant to fly away following disturbance (Martinez-Abrain *et al.* 2008).

Type of Disturbance and the Human Effects

The type, location and frequency or intensity of human disturbance due to ecotourism and recreational activities are important factors to consider with respect to their effect on colonial waterbirds. These factors are the main ones used in the determination of buffer distances or buffer zones and the implementation of spatial and behavioral restrictions on human activities. According to Miller *et al.* (2001), the type of disturbance can be correlated to the "area of influence" of humans. This area of influence varies according to different types of human disturbance; area of influence was greater for off-trail activities than for activities practiced on regular trails. The presence of dogs with humans can create greater disturbance. Joggers disturbed twice as many birds, translating into a larger area of influence, relative to people simply strolling or walking along a beach (Lafferty 2001). Pease *et al.* (2005) found that people walking and biking had a greater impact on wintering ducks than did vehicles.

The intensity of human disturbance is another key factor that can influence bird behavior. Humans are generally more easily attracted to loud noises and usually grow more curious if we see something different or strange from our everyday norms. Likewise, the similar reaction may occur in other species. For example, the sound emitted from a high power rifle will create a greater disturbance than an air rifle. Larger groups of visitors will create more noise than smaller groups, thereby causing a higher level of disturbance. Burger and Gochfeld (1998) found that loudness as well as the number of people affected the foraging rates of birds at the Loxahatchee National Park. Similarly, electric trams at the Back Bay National Wildlife Refuge in Virginia caused fewer disturbances to wintering ducks because of their relative quiet engines, when compared to the other combustion engines present (Pease *et al.* 2005).

The distance of the disturbance to waterbirds has also been suggested as one factor that can influence its effect. Logically, the closer the approach to an animal in its natural habitat, the more likely it will run away or hide. Pease *et al.* (2005) reported that birds were more severely affected by human disturbance the closer they were to the source of the disturbance. American Flamingos in the Yucatan exhibited variations in feeding activities such as alertness, flying, standing and walking according to the distances of tour boats, with flamingos spending 23% of their time on alert behavior when tour boats were around within 100 meters, compared to only 2% when they were farther away (Galicia and Baldassarre 1997).

Human disturbance caused variations in foraging rates based on the number of people present (Burger and Gochfeld 1998), the proximity of the disturbance (Stolen 2003), the amount of noise (Burger 1998; Madsen 1998) and flock size (Yasue 2005; Bechet *et al.* 2004; Mori *et al.* 2001). In all cases, human disturbance causes a reduction in the time spent feeding and increases vigilance time (Galicia and Baldassarre 1997; Yasue and Dearden 2006; Rodgers and Smith 1997). Bratton (1990) showed that responsive behavior to human disturbance may also be influenced by a bird's location, i.e. whether perched on a tree or standing in an open mudflat. Birds in better body condition usually showed a greater response to human disturbance (Beale and Monaghan 2004), flight distance varied between resting and foraging birds (Mori *et al.* 2001), and some birds took longer to resume feeding in the morning and in sites with lower levels of prey available (Yasue 2006).

Environmental Factors and Human Disturbance

The effect of human disturbance on shorebirds depends on the associated energetic cost or predation risk, and these costs are influenced by a wide array of environmental variables that operate within different spatial and temporal scales (Yasue 2006). Understanding the influence of these variables on the overall state of colonial waterbirds is very important in the design and implementation of effective management plans. The main environmental variables that may affect colonial waterbirds are habitat diversity and vegetative cover, prey availability, location of habitat, tidal flow and timing of a particular activity such as nesting, feeding or roosting.

Habitat diversity and vegetative cover are the main factors that influence the carrying capacity of a site for colonial waterbirds. For example, beaches in Thailand that had various forms of human activities and vegetation of medium height ranging between 0.5 m and 5.0 m, appeared to provide better nesting habitat than beaches with tall vegetation (Yasue and Dearden 2006). During the chick rearing stage of the Malaysian Plover, the vegetation served as foraging and hiding habitats for chicks fleeing from human disturbance. Yasué (2006) highlighted that distance to the forest cover was the only factor that affected shorebirds in their habitat selection on beaches with human disturbance. Also according to Moreno-Rueda and Pizarro (2007) physical environmental components of habitat, such as altitude, range and habitat diversity, had significant influence on bird species richness in south-eastern Spain only in heavily traversed ecotourism region, and the influence of these environmental components tend to diminish with increasing precipitation, probably due to increases in food availability.

Prey availability is another important factor that can influence the response of colonial waterbirds to human disturbance. Although Yasué (2006) suggested that distance to forest cover was more important than prey availability and human disturbance in the selection of habitats by shorebirds, the same research reported that shorebirds resumed feeding more quickly in areas of high prey availability after a disturbance event. Prey type might have been responsible for differences in flock response to human disturbance of two species, Semipalmated Plover (*Charadrius semipalmatus*) and Least Sandpiper (*Calidris minutilla*), the latter showed a reduction in foraging rates with disturbance only in areas with high amphipod density (Yasue 2005)

MANAGEMENT OBJECTIVES

Although human disturbance can have an impact on the ethological, physiological and ecological parameters of avian populations, birds have been able to adapt their behaviors and strategies, and sometimes even gain mutually beneficial rewards from human presence such as protection and provision of additional food. As Gill *et al.* (2001) highlighted, behavioral responses may not always truly reflect the consequences of human disturbance, because species that show higher levels of response may not necessarily be those that are most affected.

From a management perspective, it is essential that a thorough understanding of the target species is gained before the implementation of prescribed management strategies. Responses to disturbance may vary considerably even within a single species, evident by the different outcome of research on the same species. Factors explaining the different responses from site to site include differences in food availability, vegetative cover, and the presence of alternative feeding grounds in close proximity. In larger areas, birds will normally have more choices and options than in a small confined space. It is imperative that managers understand the actual purpose of their management strategy. Is a site being managed to protect a specific species or group of species, or is it being managed to increase the population of the species present? The answer will drive management decisions in the selection of the most appropriate approach. Strategies will also be influenced by the presence of keystone species or species that are of greater global concern.

FUTURE RESEARCH

Human disturbance research focused on the impacts on colonial waterbirds will continue to be a keen area of concern because of the increasing demand for recreational activities that encroach on habitats. More research needs to be focused on following a species (or group of species) throughout it migratory range, because the benefits and impacts in one area may not be the same as in another area. In order to truly understand a species we must be able to understand all the impacts that affect it. More research needs to be conducted on tropical species for two main reasons: first, the diversity of species in the tropics, and second, tropical regions are usually under greater threats of habitat destruction and degradation because of large movements of tourists during the colder seasons and the lure of ecotourists to these sites during the annual migration of these birds. Research in tropical areas such as the Caribbean and some regions in South America seem to have particularly lapsed.

CHAPTER 3, NESTING DYNAMICS OF THE SCARLET IBIS (*EUDOCIMUS RUBER*) IN THE CARONI SWAMP, REPUBLIC OF TRINIDAD AND TOBAGO, WEST INDIES

INTRODUCTION

The Scarlet Ibis (*Eudocimus ruber*) is a colonial waterbird of economic and cultural significance to the twin islands state of Trinidad and Tobago. This species is distributed naturally along the coast of Columbia, Venezuela, Surinam and French Guyana (Aguilera *et al.* 1993; Ramo and Busto 1988). It is also found in inland freshwater and coastal habitats throughout northern South America (Olmos and Robson 2001; Martinez and Rodrigues 1999). Although the Scarlet Ibis is a neotropical waterbird, there has been sighting of this bird as far as Texas (Sell 1918) and Colorado (Cooke 1897). Because of its bright red color, its size and active and social behavior, it has become a popular and charismatic exhibit at many zoos (Elbin and Lyles 1994), e.g. in Florida (Babbitt and Frederick 2008; 2007) and Amsterdam (Spil *et al.* 1985).

Nomadic species seem to depend on large populations to locate food and to stimulate their breeding (Frederick *et al.* 1996). The Scarlet Ibis usually feeds in groups outside the nesting site and it generally exhibits gregarious behavior throughout the seasons (Elbin and Lyles 1994). It breeds and roosts in clumps mainly of red mangroves (*Rhizophora mangle*), together with other colonial birds, such as herons and egrets (Bildstein 1990). Similar patterns have been recorded in both southeastern and northeastern Brazil (Olmos 2003; Olmos and Robson 2001; Martinez and Rodrigues 1999) and with the White Ibises (*Eudocimus albus*) (Frederick *et al.* 1996).

The Scarlet Ibis in Trinidad was considered extirpated as a breeding species in the Caroni Swamp, central Trinidad, by 1970 (ffrench and Haverschmidt 1970). Prior to that time, the Caroni Swamp population rarely nested in the same location twice, annually shifting its nesting area by a few hundred meters to several kilometers (ffrench and Haverschmidt 1970). Eventually, after the 1970s, these birds completely abandoned nesting activities in the Caroni Swamp. Evidence of nesting activities was rediscovered in 1990 by Forest Officers of the Wildlife Section of the Ministry of Agriculture, Lands and Marine Resources, which has the responsibility for the management of the Caroni Swamp (Samayah *et al.* 1990). Bildstein (1990) and ffrench and Haverschmidt (1970) suggested several possible explanations for the cessation of the Scarlet Ibis nesting activities at the Caroni Swamp, in Trinidad. None of these explanations considered the spatial dynamics of the breeding site and the intrinsic factors that could have caused the complete abandonment of the Caroni Swamp breeding site.

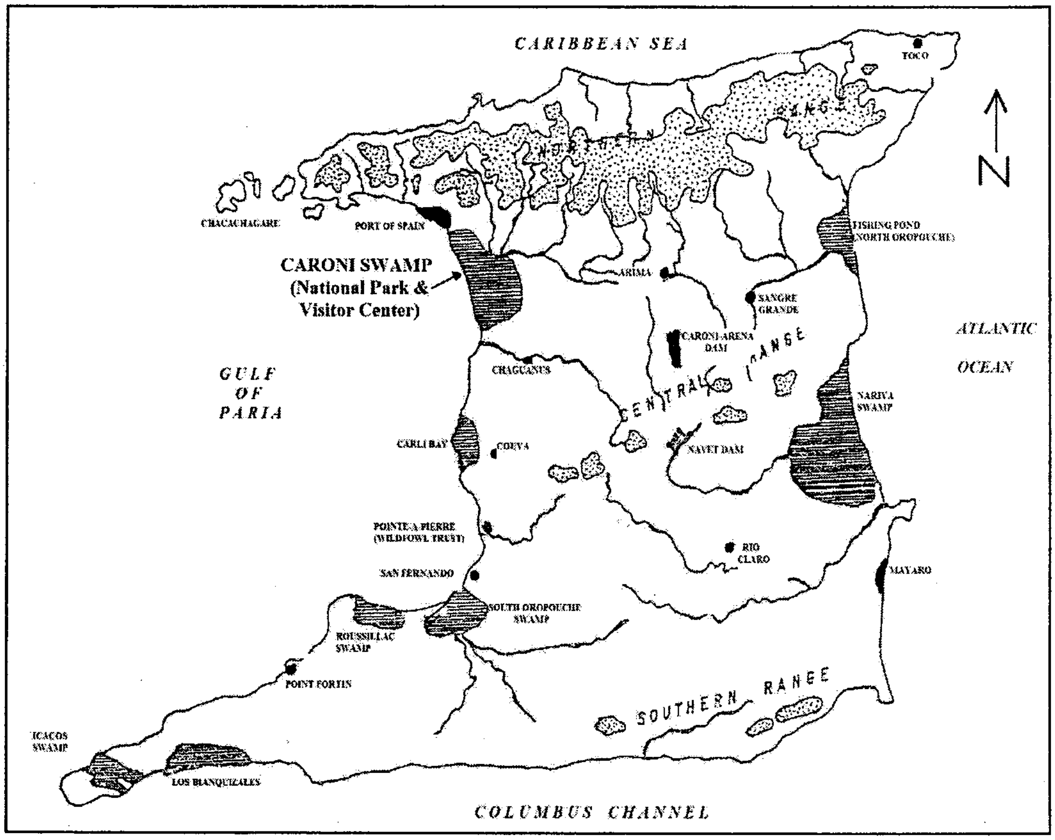
Spatial dynamics of colonial bird populations are an integral factor in their breeding success, since colonial breeding has been suggested as a strategy for reducing predation, locating food, selecting habitat, and selecting mates (Olmos 2003). Breeding colonies may also arise as a result of heritability (Brown and Brown 2000), philopatry (Frederiksen 1999), as a means of capitalizing on key weather patterns, such as arrival of rainfall (Radford and Du Plessis 2003; Whitehead and Saalfeld 2000), and for many other reasons. A strategy of colonial breeding is generally achieved through the formation of nesting aggregations, in which birds that nest in larger clusters or groups have greater reproductive success (Hernandez-Matias *et al.* 2003; Clark and Robertson 1979). The purpose of this research was to test the hypothesis that the nesting success of the Scarlet Ibis can be predicted, based on characteristics of the nest and the chosen nesting location in the Caroni Swamp, Trinidad. The situation in Trinidad will then be compared with spatial dynamics in breeding by different populations of Scarlet Ibis throughout the neotropics.

METHODOLOGY

Study Site

The Caroni Swamp, Trinidad West Indies is located in the northwestern side of the island (10° 30-39′ N, 61°25-30 ′ W), 3.5 km southwest of the capital, Port-of-Spain, and comprises 8398.1 ha, of which 5996.3 ha are protected (Figure 3.1). This area was designated a wetland of internal importance under the Ramsar Convention on July 8, 2005 (Ramsar Convention on Wetlands 2009). The swamp is an estuarine system consisting of mangrove forest dominated by red, white (*Avicennia germinans*) and black mangroves (Laguncularia *racemosa*) and herbaceous marsh. This mangrove system is interrupted by numerous channels, and brackish and saline lagoons, and is bordered by an extensive intertidal mudflat on the seaward coast (Nathai-Gyan and Juman 2005). The Caroni Swamp system falls within the Amazon-Orinoco- Maranhão complex in the Orinoco ecoregion. The climate is relatively hot and humid with an average temperature of 28°C but can reach up to 34°C, with an annual rainfall of 2110 – 3810 mm that usually occurs during the months of June to December.

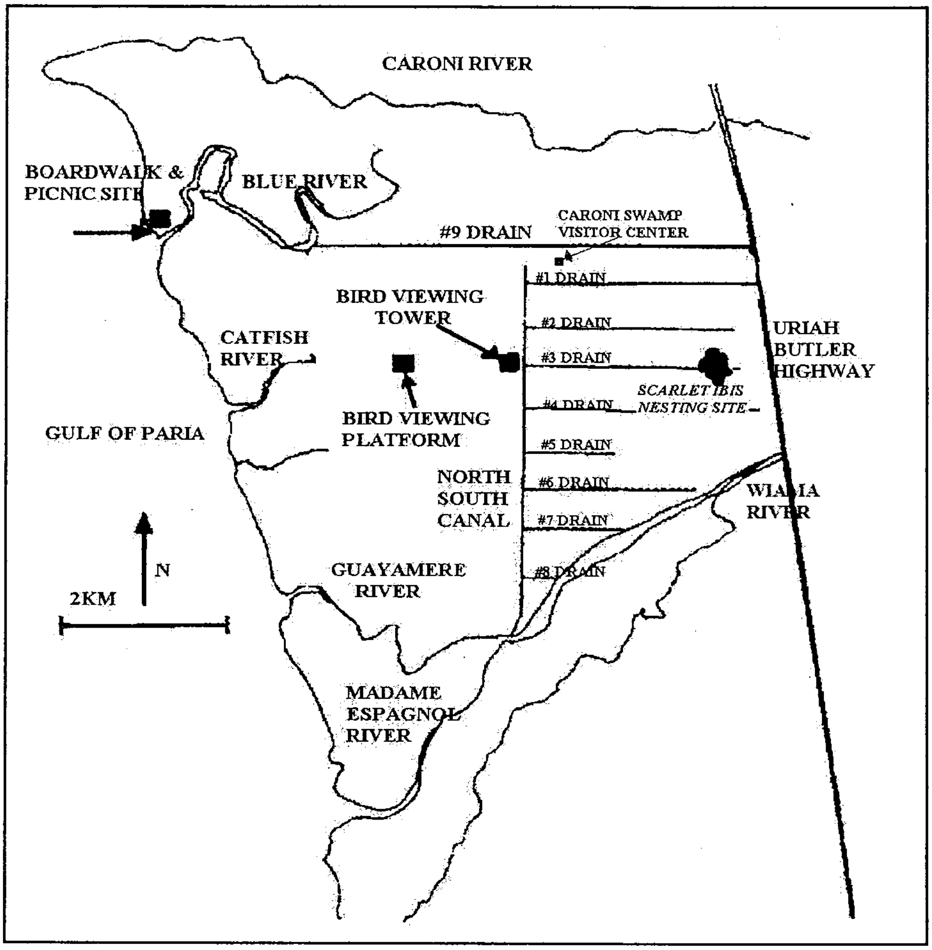
Figure 3.1 Location of the Caroni Swamp, Trinidad, West Indies.



The Caroni Swamp is bounded on the east by a major highway, which joins the north to the southern end of the island. On the south, the swamp is bounded by the Gulf of Paria and on the north and south by the Caroni River and Madame Espagnol River respectively. In the past, the swamp received sediment-laden freshwater inflow and outflow from a few surrounding rivers. However, due to some failed land reclamation schemes in the 1920s and 1950s, freshwater inflow into the swamp was reduced, leading to an increase in salinity (Bildstein 1990).

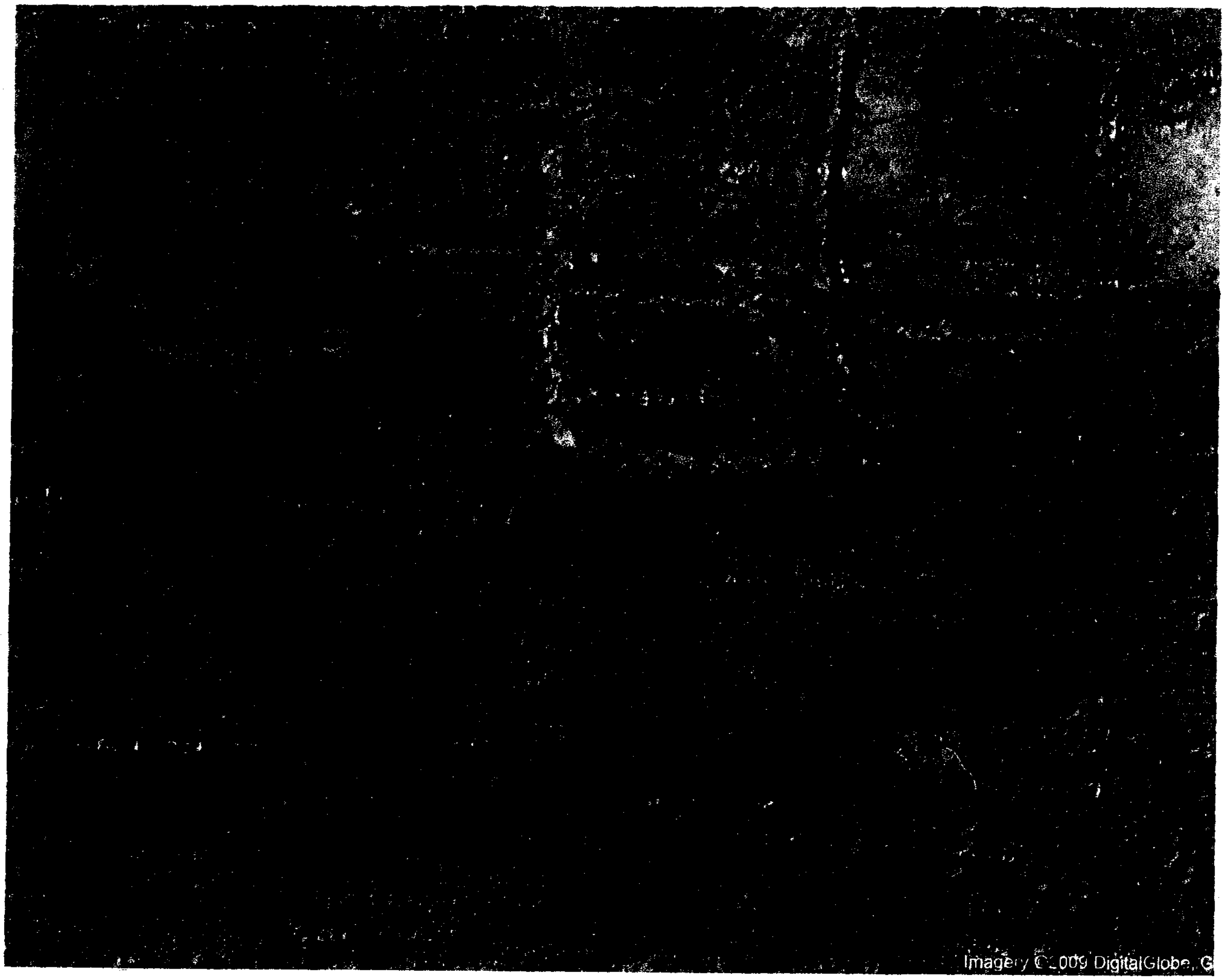
Scarlet Ibis breeding occurred during 2008 approximately 1 km from the highway on the eastern boundary, covering approximately an area of 60 km^2 with sparse patches of white mangroves, reeds and ponds (Figure 3.2). Its northern side comprises

Figure 3.2 Layout of the Caroni Swamp, Trinidad, West Indies, showing the location of the Scarlet Ibis nesting site



mainly open swamp with reeds and primary forest vegetation, such as Juniper (*Genipa americana*), Lay Lay (*Cordis sulcata*) and Gulab Jamoon (*Syzygium cumini*), and is bounded by the Waima River (Figure 3.3). On its western side is a mixture of clumps of white mangroves surrounded by water, containing areas of reed interspaced with large openings. Three sides are bounded by lands that were previously altered during the reclamation scheme of the 1950s. A major electrical corridor traverses the center of the breeding area. Scarlet Ibises were observed nesting in a mixed colony that comprised

Figure 3.3 Satillite image of the nesting location of the Scarlet Ibis nesting site in the Caroni Swamp, Trinidad, West Indies



mainly Cattle Egret (*Bubulcus ibis*), Snowy Egret (*Egretta thula*), and to a lesser extent Little Blue Herons (*Egretta caerulea*), Black-crowned Night Herons (*Nycticorax nycticorax*) and Yellow-crowned Night Herons (*Nyctanassa violacea*).

<u>Data Collection</u>

Observations occurred at the Caroni Swamp colony from April to September 2008. At the time of reconnaissance in May 2008, nests were already constructed and laying had begun. From first point of access on the northern side, we looked for areas that had high nesting activity. Because Scarlet Ibis nests seemed to be located throughout the area and interspersed with other nesting colonial waterbirds in the breeding site, we concentrated our observations to areas with higher nesting activities, regardless of species composition. Once an area was identified, crews marked the 30 closest nests in the area with numbered strips of surveyors flagging tape. Colors that were similar to objects in the environment were used to reduce disturbance. Five sites were marked on the northern side, including 18 Scarlet Ibis nests and several Cattle Egret nests. On the southern side, we undertook the same exercise and marked three additional sites for a total of three additional Scarlet Ibis nests. As data collection proceeded, any new nest found within the eight sites was tagged and recorded, adding 64 more Scarlet Ibis nests for a total of 82 nests.

To minimize disturbance, we entered each site only once per week. Recordings were taken as quickly as possible to minimize the time spent at each nest. At this time we recorded only two variables; number of eggs in the nest and number of chicks in the nest. Survival from hatching to 14 days of age was estimated as a measure of chick success, because any attempt to estimate survival longer than this time was difficult; young birds were very active and mobile and often away from their nest. For nests that were beyond sight and reach, we used a mirror attached to a long pole. Variables corresponding to the spatial characteristics of the nest sites such as height, diameter of nesting tree, distance of neighboring nests, number of nests per tree, level of cover, distance from water's edge and number of egret nests were recorded after parents and chicks had left the nest. The collection of these data followed that of Olmos (2003), reducing the effort to characterize the nest site characteristics to a total of 13 variables that showed some degree of significance in the Southern Brazil population of Scarlet Ibis, and seemed most relevant to the Caroni Swamp site during the 2008 breeding season (Table 3.1).

Table 3.1 Variables measured at the Scarlet Ibis nesting site at the Caroni Swamp in Trinidad, West Indies, during the 2008 breeding season.

Variable	**Code**	**Remarks**
Number of eggs per nest	# Eggs/nest	Highest number of eggs found per nest
Number of chicks per nest	# Chicks	Highest number of chicks observed in each nest
Height of nest	Ht of nest	High water mark based on marks on tree base
Diameter of nesting tree	Diameter	Diameter at breast height or 1.3 m
Distance of 1st closest neighbor nest	Dist N1	Distance to 1st neighbor nest (regardless of species)
Distance of 2nd closest neighbor nest	Dist N2	Distance to 2nd neighbor nest (regardless of species)
Distance of 3rd closest neighbor nest	Dist N3	Distance to 3rd neighbor nest (regardless of species)
Distance of 4th closest neighbor nest	Dist N4	Distance to 4th neighbor nest (regardless of species)
Number of nests per tree	Nest/tree	Total number of nests per tree
Level of cover	Cover	Categorical – C- Over 60% of nests covered by tree canopy, O - Under 40% of nests covered by tree canopy
Distance from the water edge	Water edge	Categorical – L – Less than 100 cm from the water edge, M – More than 100 cm from the water edge
Number of Egrets present	Egret	Categorical – A – Over 75% egrets present in the sample site, B -- Between 25 to 75% egrets present and C – Below 25% egret present

Nesting pulse	Pulse	Categorical – E – Birds nesting in first nests recorded, L – Birds nesting in nests recorded later

The number of eggs in a nest was estimated as the maximum number of eggs in the nest over the period of the study and similarly for the number of chicks. The height of the nest was recorded by measuring the distance from the point of the high tide water mark to the centre of the bottom of the nest; the diameter of the nesting tree was measured at breast height (1.3 m) from the high tide mark; the distances to the closest neighbouring nests were limited to the first four nests within a 10 m radius. This number of nests was selected based on two reasons, first because the study followed the procedure used by Olmos (2003), and second, the physical spacing of the nests were not uniform, in that, at times there were either confined in clusters or widely displaced, and difficulty arose in trying to obtain measurements beyond this distance. The number of nests per tree was based on an actual count of the number of active and inactive nests present on the tree that contained the primary nest at the time of observation, while the level of tree canopy cover was based on a visual assessment of the number of trees and the sizes of their canopies in the research area. The distance of nests from the water's edge varied considerably, and this was measured as the distance from the centre of the nest, to the edge of the low water mark on the closest embankment. However, most nests were found either within 100 cm of the embankment or on land, therefore, they were recorded as <100 cm from land. In cases were a nest was completely surrounded by water, it was recorded as ≥100 cm from the water edge. Cattle Egrets were estimated as a percent of each of 30 active nests in eight areas within the breeding colony.

Data Analysis

Data analysis followed the procedure used by Olmos (2003). Preliminary analysis included cross tabulation and Pearson Chi Squared tests to determine whether the proportion of each variable differed in predicting clutch size, success and hatchling survival to 14 days old (Table 3.2).

Table 3.2. Clutch size, number of eggs hatching in a nest and number of hatchlings surviving to 14 days derived from egg and chick counts of Scarlet Ibis during the 2008 breeding season at the Caroni Swamp in Trinidad, West Indies. The table shows how derived variables were used in the logistic regression models.

Variable	**Code**	**Remarks.**[1]	**Sample Size Used in Logistic Regression**
Clutch size	Clutchsz	An estimate of the total number of eggs laid in a nest (1, 2 or 3 eggs)	Likelihood of ≥ 2 eggs (n = 71) vs 1 egg (n = 13)
Number of eggs hatching in a nest (number of hatchlings)	Hatch	An estimate of the number of hatchlings in a nest (1, 2, or 3 chicks) independent of the clutch size; all nests are compared in a first analysis (Hatch1), then in a second analysis the subset of nests with ≥ 1 egg hatching (Hatch2)	Hatch 1: likelihood of ≥ 1 hatchling (n = 56) vs no eggs hatching (n = 26) Hatch 2: likelihood of ≥ 2 hatchlings (n = 40) vs 1 hatchling (n = 16)
Number of hatchlings surviving to 14 days	Fledge	An estimate of chick survival, based on at least two successive weekly observations[1] of one or more chicks at a nest; all nests are compared in a first analysis (Fledge1), then in a second analysis the subset of nests with ≥ 1 hatchling surviving (Fledge 2)	Fledge 1: likelihood of ≥ 1 hatchling (n = 43) vs no hatchling surviving (n = 13) Fledge 2: likelihood of ≥2 hatchlings (n = 30) vs 1 hatchling surviving

[1] One repeat observation of a chick is possible followed by fledging, but more likely followed by a chick failure, which is far less likely after two repeat observations over two weeks

Logistic regression models were then used to test the significance of the key independent variables that affected clutch size, hatching success and hatchling survival, by entering both categorical and continuous variables that passes the exploratory steps of the preliminary analysis into a model using forward stepwise regression. All tests were run in SPSS 16.0.

RESULTS

General Overview

The breeding population of Scarlet Ibis at the Caroni Swamp in Trinidad, West Indies during the 2008 breeding season was approximately 500 pairs based on estimated count while conducting field work. Total adult birds in the breeding area were estimated at approximately 3000 during the 2008 breeding season. Based on the timing of our field work, the nesting phenology of the Scarlet Ibis at the Caroni Swamp started before May and continued beyond September of 2008, when our study concluded. Mean clutch size was 1.98 ± 0.18 ($n = 82$). Sixty four percent of nests contained two eggs, while 22% contained three eggs and 13% had one egg only. Of the 171 eggs laid, 127 (74%) hatched, of which, 57% produced two hatchlings. In terms of survival success of hatchlings, 43 nests (52%) had at least one hatchling surviving to 14 days, while 37% ($n = 30$) produced two hatchlings that survived. Inclement weather conditions that contributed to fallen trees, was the major factor that influenced nest destruction.

Nesting success of the Scarlet Ibis in the Caroni Swamp depended on three key factors: distance to the fourth nearest neighboring nests, distance of the nest to the water edge, and the number of nests per tree, none of the other variables was significant.

Distance of the fourth neighbor nest and the number of nests per tree were the only variables that showed any interaction (Table 3.3).

Table 3.3. Summary of model building using forward stepwise multiple regression to predict five measures of reproductive success in Scarlet Ibis at the Caroni Swamp in Trinidad, West Indies, during the 2008 breeding season. Coefficients corresponding to the log odds ratio (B) are listed for significant variables. For variable description, see Tables 1 and 2. Combinations of two and three – way interactions among all predictor variables were tested in addition to their main effects; except where indicated, interaction terms did not enter models.

Response Variable	Not Entering Model	Entering and Leaving Model	Entering Final Model	B (S.E.)	P	Overall Model Statistics
Clutchsz	Pulse	Egret	Nest/tree	0.25 (0.10)	0.017	R^2 = 0.18, p = 0.014
Hatch 1	Diameter, Dist N1, Dist N4, Nest/tree, Water edge	None	None	------	------	-------
Hatch 2	# Eggs/nest, Ht of nest, Diameter, Dist N1, Dist N2, Dist N3, Nest/tree, Cover, Egret, Pulse	None	Water edge Dist N4	0.011 (0.004) 2.03 (0.08)	0.007 0.001	R^2 = 0.23, p = 0.008
Fledge 1	# Eggs/nest, Ht of nest, Diameter, Dist N1, Dist N2, Dist N3, Nest/tree, Cover, Egret, Pulse	None	Dist N4	0.007 (0.003)	0.010	R^2 = 0.10, p = 0.010
Fledge 2	Nest/tree, Water edge, Cover, Egret	None	Nest/tree **X** Water edge	0.21 (0.08)	0.008	R^2 = 0.29, p = 0.002

Distance of Neighboring Nests

The distance of four closest neighboring nests that were <10 m in distance varied between 20 and 831 cm. Although several measures to the first, second, third and fourth nearest nests were tested in the stepwise regression, the distance to the fourth closest nest was the only significant predictor of hatching and fledging success, with a significant interaction with distance from the water's edge for hatching success (Table 3.3). Comparing cases of two or more eggs hatching to cases of just one egg, success was better for nests located closer to the fourth nearest nest, providing these nests were <100 cm from the water's edge (Figure 3.4). Comparing cases of no hatchling surviving to 14 days old to cases of one or more hatchling surviving, success was better for nests closer to their fourth nearest neighbor (Figure 3.5).

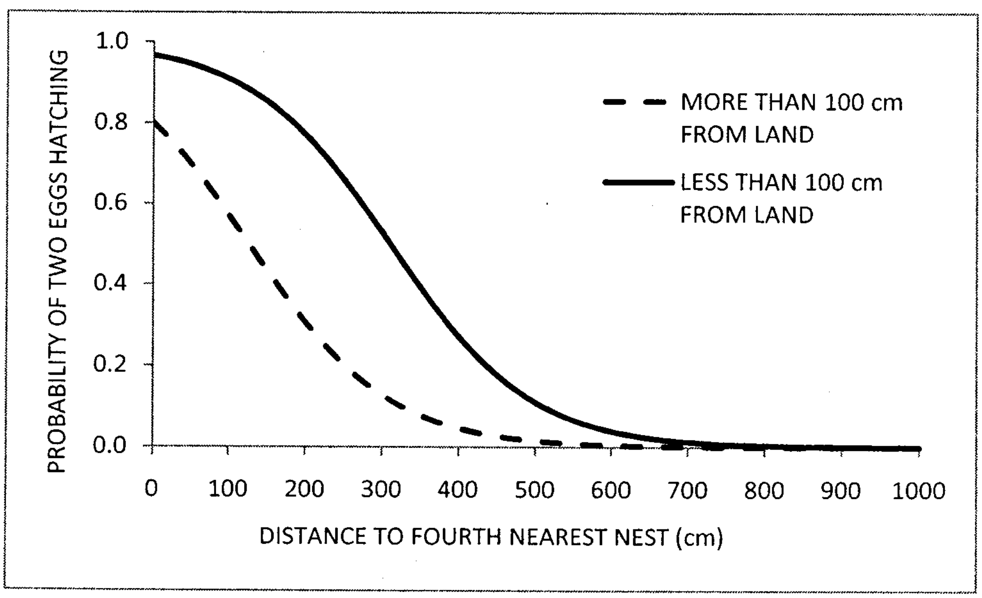


Figure 3.4. Probability of two eggs hatching verses one as compared in relation to the distance of the fourth nearest nest in the Caroni Swamp, Trinidad, West Indies.

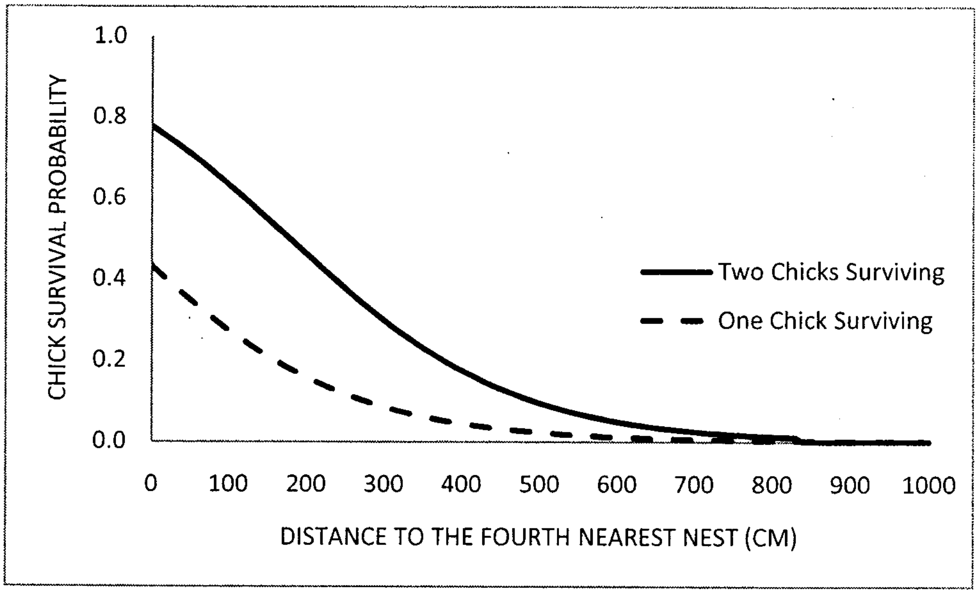


Figure 3.5. Probability of chick(s) surviving up to 14 days old in relation to the distance of the fourth nearest nest in the Caroni Swamp, Trinidad, West Indies.

Number of Nests Per Tree

Between one and 16 nests occurred per nesting tree. Among nests that only contained one egg, 91% were built in trees with fewer than five nests. The number of nests per tree was the only significant predictor of clutch size (Table 3.3). Both clutch size (Figure 3. 6) and fledging success (Figure 3.7) were higher for nests on trees with more conspecific nesters, provided for fledging these nests were <100 cm from the land.

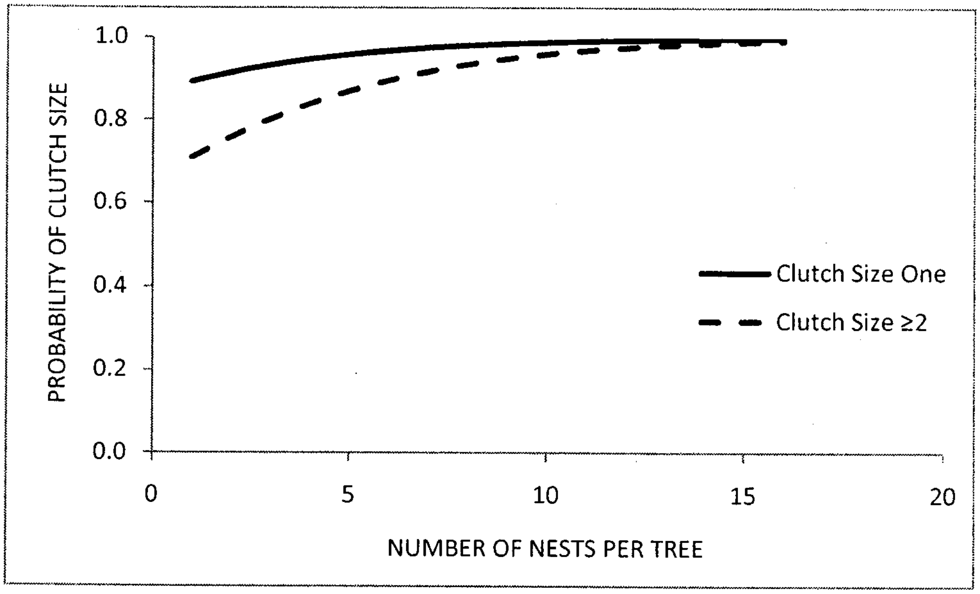


Figure 3.6. Probability of Scarlet Ibis clutch size in relation to the number of nest per tree at the Caroni Swamp, Trinidad, West Indies.

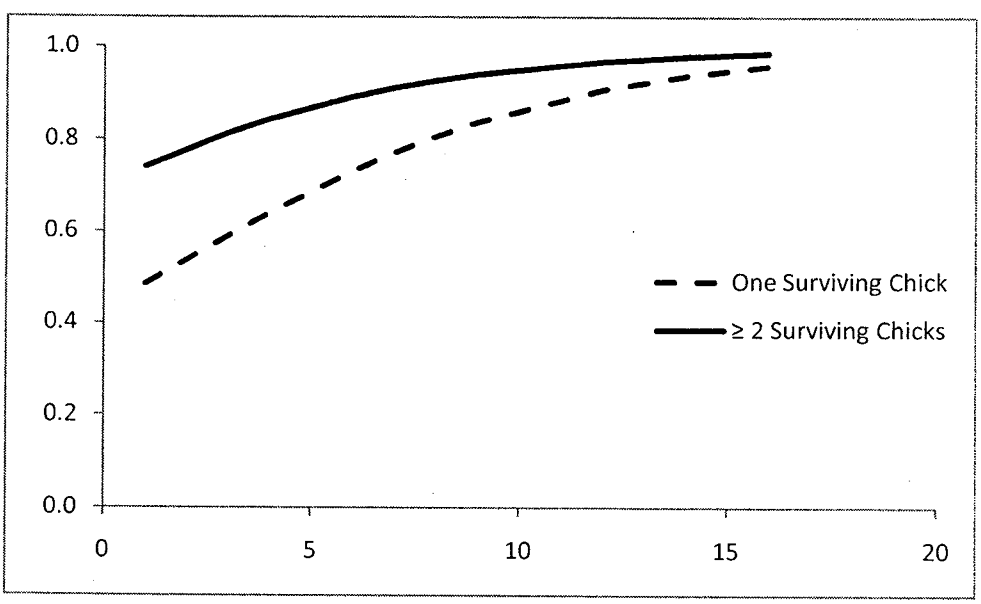


Figure 3.7. Probability of Scarlet Ibis chick(s) surviving up to 14 days old in relation to the number of nest per tree in the Caroni Swamp, Trinidad, West Indies.

Distance to Water Edge

The distance of the Scarlet Ibis nest to the water's edge varied from 0 to 488 cm. This variable was separated into two broad groups: nests that were ≤100 cm from the water edge and nests that were ≥100 cm from the water edge. Seventy three percent of nests were located ≤100 cm. Distance to water's edge was a significant predictor of both hatching and fledging success (Table 3.3).

Nesting Pulse

The first pulse of nesting corresponded to the first set of nests marked between May and July, and the second with the second set from July to September. A third nesting pulse was not observed. Nesting pulse was not a predictor of clutch size ($X^2 = 3.670$, $df = 2$, $P = 0.160$), although second pulse nests had five times as many nests with three eggs than the first pulse (n = 18), and four times as many nests with two eggs as compared to the first pulse (n = 53). Nesting pulse was tested in models of hatching and fledging (Table 3.3), where no significant relationships were found.

DISCUSSION

Colonial breeding and nest aggregation are techniques used by birds to guard against aerial nest predation (Hernandez-Matias *et al.* 2003). This implies that colonial birds will usually choose nesting sites with heavy cover. Although Olmos (2003) concluded that nest cover was significantly correlated with the success of the nest in southern Brazil, this was not the same for the Scarlet Ibis at the Caroni Swamp. Unlike nesting population of Scarlet Ibis in northern and southern Brazil (Olmos 2001; Martinez 1999), predation was not a significant contributor of nest failure in the Caroni Swamp, in fact, pre hatching nest failure due to predation was minimal, as there were no evidence or observation either aerial or surface predators in the heronry, similar to observations by ffrench (1970). Low occurrence of aerial predators could be explained by the location of the breeding area in close proximity to a major highway and under the line of the flight zone for the country's international airport, which causes a fair amount of air traffic. However, based on observations made during the course of this research, the main cause of nests collapsed was due to a combination of heavy rainfall and loosening of the nesting material caused by the high movement of fledglings from one nest to another.

The closeness of nest to the water's edge proved to be an important factor in the breeding success of the Scarlet Ibis at the Caroni Swamp. An example of this is found in the breeding behavior of the sociable Weaver Birds (*Philetairus socius*), which builds communally clustered nests at distances of 200 and 300 m from water, while at further distances, nests are regularly distributed (Giesselmann 2008). This behavior of nesting in clusters closer to the land, can also be identified in the nesting patterns of the Scarlet Ibis in the Caroni Swamp, where higher nesting density were found in areas closer to the water's edge, an explanation may be that more regular distribution of nests further from the water's edge is due to competition and/or territoriality among birds further from foraging areas. Although territoriality has never been suggested in description of breeding in the Scarlet Ibis, or in any other species in the family, such as the White Ibis, competition can be prominent in colonial waterbirds (Johnston 1985; 1984; Frederick 1982). The best nesting spaces should afford the most protection for young birds, as well as an abundant food supply. Nesting sites closer to the water's edge at the Caroni Swamp may be better in terms of acquiring food quickly and returning to the nest in order to feed and protect the hatchlings.

The strategy of nesting in pulses or at different times is very common in birds. Nest density and the timing of these pulses are strongly correlated with variations in the timing of the onset of the rainy season in Magpie Goose (*Anseranas semipalmata*) in monsoonal northern Australia (Whitehead and Saalfeld 2000). The onset and intensity of the rainy season can play a pivotal role in the reproductive success of colonial birds because it may influence food availability, energy expenditure of flight, the cost of thermoregulation, changes in timing of nesting, clutch size and even major perturbation such as the failure of a large population to nest for an entire year or breeding season (Radford and Du Plessis 2003). (ffrench and Haverschmidt 1970) suggested that the Scarlet Ibis in Trinidad initiated breeding soon after the onset of the rainy season, and found a similar pattern in Guyana, but there was no mention of distinct nesting pulses in his research. (Olmos 2003; 2001) found distinctive nesting pulses with the Scarlet Ibis population in Brazil during his study which was conducted during October 1996 to March 1997 however, this period did not coincide with the peak rainy season, which was during March.

Although breeding early usually translates into greater overall success and survival of chicks, there are several other important interactions between egg quality, parental quality and early laying that may affect breeding success (Arnold *et al.* 2006). Whitehead and Saalfeld (2000) suggested that clutches of egg in later nesting pulses usually contained fewer and smaller eggs; this was not the case in Trinidad. In fact, nesting pulses had no significant effect on the total number of eggs laid per clutch, whereas second pulse nest actually had more clutches with three eggs and greater hatching and fledging success. (Olmos 2003, 2001) concluded that second and third pulses nest were less successful, but it was due mainly to predation and nest destruction by storms, rather than smaller clutch sizes. It seems likely that the success of the second pulse nest in Trinidad was due to unusual weather patterns during the 2008 breeding season. Follow-up investigation of the breeding area in May 2009 revealed that there were ≥500 Scarlet Ibis chicks already about 2 to 3 weeks old and moving from branch to branch quite easily. During this period, there was only intermittent rainfall of low intensity.

Although the height of a nest may be an important factor in the avoidance of aerial predation (Olmos 2003, 2001), this was not the same for the Scarlet Ibis in the Caroni Swamp in Trinidad. Given the erratic weather patterns and the low level of natural predators during the 2008 nesting season, positioning nests low may have been more a strategy to protect the nest from heavy rainfall and strong winds, because during the course of field work, a few large mangrove trees were blown down following heavy rains. Similarly, Olmos (2003, 2001) stated that nests nest tree height was negatively associated with nesting success in Southern Brazil.

The diameter of the nesting tree was not a significant factor in the nesting success of the Scarlet Ibis at the Caroni Swamp, in Trinidad. During a preliminary assessment of the breeding area in1990, nests were built on much larger trees, mainly of red mangrove (Gil-Delgado *et al.* 2005; Gomez *et al.* 2001; Samayah *et al.* 1990); in the present study, nests were built on much smaller trees, mainly white mangroves. This difference has probably developed due to the movement of the 1990 rookery from pristine primary mangrove vegetation, to secondary growth located on the outskirts of the swamp.

The number of nests per tree was one of the most significant factors that influenced the laying and hatching success of the Scarlet Ibis in the Caroni Swamp. Olmos (2003, 2001) raised the issue of the "selfish herd effect" and its influence on the association between nesting success and nesting density with regards to the different pulses during the breeding season. This "selfish herd effect" suggest that, the survival of individuals is directly related to the number of individuals in the group and their proximity to each other it further suggests that in cases with lower nesting aggregation, there will be more losses due to predation (Hamilton 1970).This selfish herd effect is more applicable in cases where predator-prey relationships are prominent. Because evidence of natural predators was minimal at the Caroni Swamp, the aggregation or clustering of Scarlet Ibis nests cannot be explained as a consequence of protection against predators. However, nesting in colonies has been suggested as a form of social behaviour in birds, that can be modified due to the adaptive nature of particular species and can result in both positive and negative benefits to the group and individual (Oro 1996). Clustering of nests may also be due to philopatry and heritability (Brown and Brown 2000; Frederiksen and Petersen 1999). For example, Frederiksen and Petersen (1999) suggested that first time nesters usually select their nesting site based on their instinctive assessment of the quality of a site deduced from the breeding success of other conspecifics at a site. Because this information is not perfect, birds tend to nest closer to their natal site.

Colonial birds may also nest in clusters because of their physical fitness, with the less fit birds being excluded. This attribute of fitness may be related to age or state of an individual (Wendeln and Becker 1999). In the Caroni Swamp, there was a greater likelihood of having two or more eggs in nests that were clustered when compared to those nests that were spaced out, possibly linked to the fact that female birds that are older and more experienced, are more likely to nest early and are less likely to lose their clutches (Hipfner 1999). Unfortunately, laying replacement clutches or double brooding in Scarlet Ibis has never been observed, though (Gomez *et al.* 2001) thought the practice of double-brooding is likely to occur in similar species such as the Boat-billed Heron (*Cochlearius cochlearius*), which produces two distinct clutches, during the dry and wet seasons.

A comparison of the breeding biology of the Scarlet Ibis at Caroni Swamp in Trinidad and other populations throughout the neotropics, such as northern and southern Brazil (Olmos 2001; Martinez 1999), Surinam (ffrench 1970) and Venezuela (Ramo 1988) revealed almost similar patterns. Throughout the neotropics, Scarlet Ibis seem to initiate breeding at the onset of the rainy season; however this period varies from one location to another. Their average clutch size comprised of two eggs. The major source of nest failure was predation and unfavourable weather conditions, however, in Trinidad, the latter was more significant. Although the Trinidad Scarlet Ibis population was the smallest in the neotropics, they showed the greatest reproductive success probably due to the presence of few natural predators. Unlike the population in southern Brazil that showed greater success when breeding early in the season, the Trinidad population had more nest with larger clutches during the second pulse in the 2008 breeding season.

CHAPTER 4, GENERAL CONCLUSION AND RECOMMENDATIONS.

The effects of human disturbance on colonial waterbirds are a critical component of any management strategy which seeks to develop sustainable relationships between human use and wildlife. Although based on a literature review, it was evident that there were little or no differences on the effects of human disturbance on colonial waterbirds based on biomes, habits or functional grouping, and it was clear that there was a lack of published research on colonial waterbirds in tropical areas. Tropical biomes have the greatest diversity, are considered hotspots for endemic species and account for approximately 74% of the bird species (Birdlife International 2008), more research should be conducted in these areas.

The major focus of research on the effects of human disturbance tends to concentrate on the reproductive physiology of colonial birds. This reproductive physiology is important, because it determines the success of a population and is usually initiated by the change in environmental conditions: winter to summer in temperate regions and dry to wet season in tropical regions. Presently, there is unpredictability in the timing of annual changes in weather both in tropics and temperate zones, which can lead to a greater inconsistency in timing of nesting events by making it difficult for adults to select optimal time to initiate breeding and nesting success. Therefore, more research should be conducted on the effects of environmental changes on the breeding success of both tropical and temperate species of colonial waterbirds. One step further would be to look at species with similar phylogeny and life histories in order to better understand these effects of environmental changes across biomes. An example of such environmental unpredictability was evident in the breeding season of the Scarlet Ibis in the Caroni Swamp, in Trinidad. During the 2008 breeding seasons only a few Scarlet Ibis nests and hatchlings were observed by late June. During a follow-up visit to the heronry in mid May 2009, ≥300 nests with approximately 500 hatchlings were observed. Such variation in the timing and number of nests and hatchlings may be attributed to the timing of local weather pattern changes.

The Scarlet Ibis is one of many species of colonial waterbirds. This bird is of special interest to the island of Trinidad, West Indies because of its economic, national and cultural significance. The Scarlet Ibis is considered as the focal point of the country's ecotourism industry and a symbol of national identity. Faced with numerous problems, the Scarlet Ibis has not been afforded the necessary protection because of a lack of understanding of its life history, breeding physiology and behavioural patterns, because of inadequate and outdated management practices, and because of a lack of current and updated information on the species. In order to address this issue, more research needs to be carried out on the population status, migratory pattern and breeding biology of the Scarlet Ibis in the Caroni Swamp. Such research would help to understand the issues of philopatry, double brooding, and re-nesting as they relate to this species. Research also needs to be carried out on the selection of nesting sites, in order to determine what constitutes a suitable nesting site, so as to prevent future nesting site abandonment. Research of this nature cannot be undertaken immediately, therefore, in the interim, the knowledge gained from this study with respect to the importance of nesting clusters, closeness to the water's edge and nearness of neighbours can be used to develop new management strategies for promoting future sustainability. Such strategies could entail the development of buffer zones around breeding sites, protection of key feeding areas, and increased public education.

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