INFLUENCE OF HABITAT ON THE OCCURRENCE OF THE ENDEMIC BARBUDA WARBLER (*Setophaga subita*) AND RESIDENT YELLOW WARBLER (*S. petechia*)

by

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Bachelor of Science, University of the West Indies, 2010

A Thesis in Partial Fulfilment of the Requirements for the Degree of

Master of Science in Forestry

in the Graduate Academic Unit of Forestry and Environmental Management

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This thesis is accepted by the

Dean of Graduate Studies

THE UNIVERSITY OF NEW BRUNSWICK

May 2018

ABSTRACT

The Barbuda Warbler (*Setophaga subita*), endemic to Barbuda, Lesser Antilles, and resident Yellow Warbler (*S. petechia*) are known to co-exist in at least some areas on Barbuda; but since little else is known of these species' ecology on the island, much more groundwork is needed. This study explored (i) spatial and temporal distribution; (ii) seasonal patterns of breeding and moult; and (iii) patterns of habitat use, of both warbler species on Barbuda. Gathering these data required extensive island surveys of both species conducted over four month-long field trips. Mist-netting and colour-banding target warbler species revealed information on demography, breeding and dispersal. The distribution of each species was found to be non-random. Point-count data analysis revealed that the Barbuda and the larger Yellow Warbler used slightly different physical resources; Barbuda Warblers occur in negative association with Yellow Warblers, but Yellow Warbler distribution was not found to be influenced by Barbuda Warblers. Along with their respective processes of habitat selection, interspecific interactions may contribute to their ecological separation. Both species were found to breed almost at the same time, in months of May and June, a pattern consistent with most North American Passerines.

ACKNOWLEDGEMENTS

I thank the following for their contribution to this experience…

Angela	Codrington	Jack	Ludwig	Ryan
Anjie	-N. Parks	Jawara	Majel	S.J.
Arthur	Dayo	Jenn	Marina	Sakej
Asif	Dolores	Johnson	Marylin	Shakti
Barb	Din	Noseworth	Matt	Sharlene
B. Council	Dove	y	Michael	Sheldon
Barney	Duma	Jude	Mike	Shiva
Bethany	Edee	Karl	Naranjits	Spasaqsit-
Bob	Elias	Kchiknatch	Nickel	Possessom
Brain	Elizabeth	t	Pam	Srishti
Francis	Eva &	Keegan	Peter	Stanislav
Brett	Vance	Ken	Pooran	Theophilus
Stewart	Floyd	Kern	Profit	Trent
Buffy	Gail Paul	Kevin	Pumpkin	Troy
Caitlin	Gene	Kiew-nik	Raj	UNB
Chris	Graham W.	Kim	Ravi	Vasudeva
Clem	Graham H.	Kris	Rob	Vince
Clive	Hart	Larisa	Robin	Vishnu
	Hugh	Lisa	Rock	

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CHAPTER 1

INTRODUCTION

Background

The Barbuda Warbler (*Setophaga subita*) is a species of bird endemic (geographically restricted) to the island of Barbuda, part of the sovereign state of Antigua & Barbuda in the Lesser Antilles of the Caribbean. The species was formerly considered one of three subspecies of the Adelaide's Warbler (*S. adelaidae*) (now a Puerto Rican endemic); the other (endemic) form occurs on the island of St. Lucia (*S. delicata*) (Figure 1.1). The full species status classification of these three (now regarded as part of a superspecies - a group of species, geographically separated, that share a common ancestor), formerly based on morphological criteria, is now based on molecular-genetic criteria (Lovette *et al*. 1998; Curson 2017). The current genus name *Setophaga* has nomenclatural priority over its former genus *Dendroica* arising from a molecular phylogenetic revision of the family Parulidae (Lovette *et al*. 2010; AOU 2011).

IUCN (2014) lists the Barbuda Warbler's conservation status as "Near Threatened," and suggests a decreasing population. This status is reasonable considering the species' restricted range and small population size of 1000-2500 individuals (del Hoyo *et al*. 2010). However, no monitoring of density or population was conducted for this status assessment, and, with adequate data, the status of the species can be more definitively determined.

Previous work

There have not been comparative studies illustrating differences in use of structural features of habitats occupied by Barbuda, St. Lucia and Adelaide's Warblers.

Einarsson (2007) and Diamond (2011) have studied the Barbuda Warbler since the time that Lovette *et al*. (1998) raised it to species status. The paucity of previous field studies on the Barbuda Warbler may be attributed to its presumed biological similarities to Adelaide's Warbler. Beyond these recent works, studies mentioning the warblers are few and, notably, sites in Barbuda (Bond 1928, 1930; Danforth 1935a; Diamond 1973; Suarez-Rubio and Thomlinson 2009). From a literature search (completed 6/04/2013), 48 publications contributed to what is known about these three species. Even after gaining endemic status, there was little commitment to the study of the Barbuda Warbler. A comparison of relative coverage in the literature surveyed illustrates a need for better insight into the ecology of the Barbuda Warbler (Figure 1.2).

Physical environments where the closely related endemic *Setophaga* warblers occur differ across the islands of Barbuda, Puerto Rico, and St. Lucia (Toussaint *et al*. 2009; Toms 2010a, b; Diamond 2011). Each species selects a different suite of environmental resources (Toms 2010a, b; Diamond 1973, 2011); Diamond (2011) recently observed that the Barbuda Warbler is present in "xeric scrub and dry forest, and apparently less common in mangroves and dense, low coastal bush." The warbler is also found in the developed areas around Codrington Village (Diamond 2011; pers. obs.). Table 1.1 summarizes the occurrences of the three endemic warblers among the habitats on the islands according to Diamond (2011) and Toms (2010).

Comparing the (then conspecific) warblers' use of habitats in St. Lucia and Barbuda, Diamond (1973) reported a peculiar pattern in their distribution across different habitat types. The Adelaide's Warbler appeared to be widespread on St. Lucia but replaced by the Yellow Warbler (*Setophaga petechia*) in arid scrub; however, the

Adelaide's Warbler and the Yellow Warbler co-existed in arid scrub on Barbuda (Diamond 1973). Studies of interspecific interactions between Barbuda and Yellow Warblers on Barbuda may help characterize the warblers' niches.

In a study on Barbuda, Einarsson (2007) recorded Barbuda Warblers responding to the song of the Yellow Warbler at a site situated on the east coast of the island. His results also suggest that both warbler species may share a niche, and appealed for studies that reveal the warblers' interspecific interactions.

The resident population of Yellow Warblers in the Lesser Antilles has also received little scientific attention, apart from their co-existence with Barbuda Warblers in dry areas on Barbuda (Diamond 1973, above). It seems reasonable to expect that there may be some overlap in use of resources between the two warbler species on the island.

Since little is known of the ecology of this single-island endemic (Diamond 2011), much groundwork is needed on the demography, life history, and general ecology of the bird both to facilitate comparative studies on the species and to guide conservation plans on Barbuda. Given the vulnerability associated with endemism, attempts to conserve habitats which support the warbler's persistence may be necessary. The information gathered from this study can be used to highlight the areas that are associated with the Barbuda Warbler, and hence facilitate identification of potentially suitable warbler habitat, and guide land-use and development decisions on Barbuda.

As I attempt to document the overlap in distribution between Barbuda and Yellow Warblers, I have included the possibility that interspecific interactions between them potentially influence each other's occurrence.

Because habitat selection potentially varies across the annual cycle, I attempt to also document breeding cues (Diamond 1974; Gunn *et al*. 2000) along with measurements of pre-selected variables (e.g. canopy height and coverage, dominant tree species, temperature (DeGraaf 1998)). For conservation purposes, it is useful to know what resources are selected when birds are breeding.

Objectives

I explore the extent to which there is a pattern of habitat use that accounts for the majority of the distribution of the Barbuda and Yellow Warblers across the island. The assumption that habitat use influences species occurrence corresponds to findings from Robinson and Holmes (1982), Sabo and Holmes (1983), and DeGraaf *et al*. (1998), which suggest that constraints imposed by vegetative structure influence patterns of bird habitat selection and resource exploitation, and hence distribution.

My research specifically:

1. Documents and compares the current distribution of Barbuda and Yellow Warblers on Barbuda

2. Estimates what physical resources of the environment are selected by Barbuda and Yellow Warblers across their breeding seasons on the island; and

3. Estimates the timing of Barbuda Warbler breeding seasons

This thesis is organised in a traditional format, where Chapter 1 provides background information of relevant studies and site description. Chapter 2 briefly summarises methods that are used in the field, and provides justification of the methods used in this study. Chapter 3 addresses the habitats and distribution of the two species. The specific procedure is presented, giving details of island-wide surveys of both species which

recorded the presence and number of warblers (objective # 1), and component habitat attributes at GPS-referenced sample-stations (objective # 2). Chapter 4 gives details of mist-netting and colour-banding procedures, and describes the seasonality of breeding and moult. I emphasise that data presented in this chapter were recorded from studying the target warbler species for only one calendar year; but observations of banded individuals during survey months yielded clues which helped to estimate timing of annual cycles (objective # 3). Chapter 5 provides a general discussion, synthesising the discussions from the previous chapters.

Site Description

Barbuda

Climate

The research was conducted on the island of Barbuda, located in the outer Leeward Islands of the Caribbean, at roughly 17° 35’ N and 61° 48’ W. It is a limestone island, measuring approximately 161km2. Annual rainfall and temperature are illustrated in Figure 1.3. The annual mean rainfall is 924 mm. The mean temperature during the hotter, dry season months is 27°C, and 25°C during the cooler months of December to February (McSweeney *et al*. 2012; OpenStreetMap Project 2017).

The island is under the influence of strong and constant easterly trade winds throughout the year but relief and orientation account for local wind variations. Heavy rainfall associated with hurricanes and tropical storms contributes significantly to wet season rainfall totals (McSweeney *et al*. 2012).

Physiography

Figure 1.4 shows broad physical characteristics and landforms of the island. The coastline is dominated by sandy shores, forming narrow beaches along much of the eastern, windward coast. Extensive beaches, dunes, and mangroves fringe the western and southern coastal areas. The Codrington Lagoon, 35 km2 (WIATT Institute 2013), spanned almost entirely the western side of the island during this project (but was breached during Hurricane Irma, September 5-6 2017). Barbuda is generally flat, with slightly raised coralline limestone platforms to the east that increase in height eastward and northward to form the "Highlands". The Highland region is characterised by a steep slope (often an abrupt cliff) on the north and east, and a gentle slope on the south and west (McSweeney *et al*. 2012). Though the limestone formation of the Highlands is similar to that of the lowlands, the topsoils differ between the two landscapes. There are also large sinkholes, such as Darby's Cave, from which tall trees emerge. No watercourses flow on the plains, but shallow ponds, wells and other depressions often contain standing water. Some of these, e.g., Bull Hole, are large and support fresh-water swamp vegetation (Harris 1965).

Vegetation

Evergreen woodland is the most extensive vegetation type on the island. Seldom exceeding 10m in height, it consists of trees and shrubs with small, simple, leathery leaves. The woodland vegetation occurs in two or three strata. Closed-canopy stands are more extensive in the Highlands compared to the woodland of the marginal plain, which by contrast is more open, and features a more distinct shrub layer. The shrubs are xerophytic, adapted to the arid conditions of the region. On the steep slopes at the

windward edge of the Highlands, there are patches of higher woodland. White cedar (*Tabebuia pallida* Lindl.), loblolly (*Pisonia fragrans* Dum. -Cors. and *P. subcordata* Sw.), whitewood (*Bucida buceras* L.) and turpentine (*Bursera simaruba* L. Sarg.) are the dominant deciduous forest trees within the Highlands. The structure and composition of the woodland differ between the Highlands and the plains presumably because of soil type and land use (Harris 1965).

A few relatively small grasslands occupy the flattest surfaces and are a mixture of native and introduced species. A wide variety of herbaceous plants occurs in association with the grasses, bordering thickets of thorny shrubs on gentle slopes. The grasslands are mainly within the widespread evergreen woodland and are presumably the result of land clearing or fires. The extreme southeast of the grasslands is fringed with whitewood trees and consist almost exclusively of *Paspalum bakeri* (Hook.) (Harris 1965). Beard (1949) considered this grassland type to be the only natural savannah in the Lesser Antilles, a result of soil conditions unfavourable for tree and shrub growth.

The coastal communities vary in stature from grass and prostrate shrub growth to woodland. Harris (1965) recognized four distinct types: Manchioneel groves, mangrove swamp, strand vegetation, and rock pavement vegetation. The Manchioneel (*Hippomane mancinella* L.) is the most common tree of low, sandy, muddy coasts, reaching up to 10 m in height, forming groves with *Acacia*, gut apple (*Annona glabra* L.), and sea grape (*Coccoloba uvifera* (L.) L.) on the leeward coasts of the island at the edges of the lagoon and salt ponds. The mangrove forest community fringes sheltered bays, creeks, and lagoons of the leeward coasts, and consists of red (*Rhizophora mangle* L.), white (*Laguncularia racemosa* (L.) Gaertner f.), black (*Avicennia germinans* (L.) L.), and

button mangrove (*Conocarpus erectus* L.). Much of the mangrove's edge forest consists of logwood (*Haematoxylum campechianuum* L.) and *Pithecellobium unguis-cati* L. The red mangrove occupies the seaward side, though less extensive on the windward coast of the island. The black and white mangroves occur in shallower water behind the zone of red mangrove, and the white mangrove occupies the dry foreshore. Morning glory (*Ipomoea sp*.) and sea bean (*Canavalia maritima* Thouars.) extend across the beach in association with low grasses and succulents (Harris 1965). Inland from the southern and western shores, the sand dunes are stabilized by maritime scrub which forms a low growing, patchy mat of vegetation (McSweeney *et al*. 2012). Expansive areas of limestone pavement, mainly on exposed windward coasts, feature sparse vegetation of spray-tolerant dwarf shrubs and cacti. The most characteristic are *Strumpfia maritima* (Jacq.), *Mammillaria nivosa* (Link ex Pfeiffer), and *Melocactus intortus* (Miller).

Habitat degradation

Most of Barbuda's natural habitats have been degraded by residential and commercial development, traditional charcoal production, shifting cultivation, development of plantations, grazing and browsing by livestock, and timber harvesting. Complete or partial clearance and fires have direct destructive effects on plant and animal communities, and on soils. Feral and domestic livestock (mainly donkeys) have roamed uncontrollably over large areas for decades. The ecology of the marginal plain is disturbed by widespread grazing and trampling, removal of organic matter, selective browsing of palatable species, and the dispersal of other species (Harris 1965).

The vegetative associations and diversity are as described by Beard (1949) and Harris (1965); however, present-day surveys of the vegetation and landscape are

necessary to update the historical accounts, as anthropogenic development, farming, and browsing from feral livestock have persisted for decades. The understorey is not well defined across the greater Barbudan landscape, except in the dry expansive Marginal Plains, where it often occurs as a coarse, 1-2 m high layer amidst a 3-5 m grove. The expansive dry scrub of the lowland plains is characteristically thorny and of low foliage density. This contrasts with the densely foliated but fragmented Highland mixed-species vegetative associations, often one stratum, and less than 10 m high. Mangrove growth was distributed across both wet and dry areas. Samples where *R. mangle* dominated were often taken next to the stand, to avoid spending much time and effort scrambling over the dense tangle of roots, and most of these stands occur in water. *L. racemosa* and *C. erectus* sometimes occur uncharacteristically in relatively dry areas, nowhere near moist soil or water. This detail can blur the distinction between mangrove growth and arid scrub for a researcher, as the dry mangrove growth supports many of Barbuda's lowland scrub species.

Standing freshwater is scarce on the island, and indeed was absent near most of the sample points. Most sampling days were hot and dry; it is unlikely that the vegetation, at least at the sample points, retained any pools of water on its surface at the time of the observations.

Chapter 2 presents a general picture of bird sampling methods, and introduces the methods used in this project. Design of the structure of the point-count and mist-net sampling regimen used is described and justified according to the Barbudan landscape

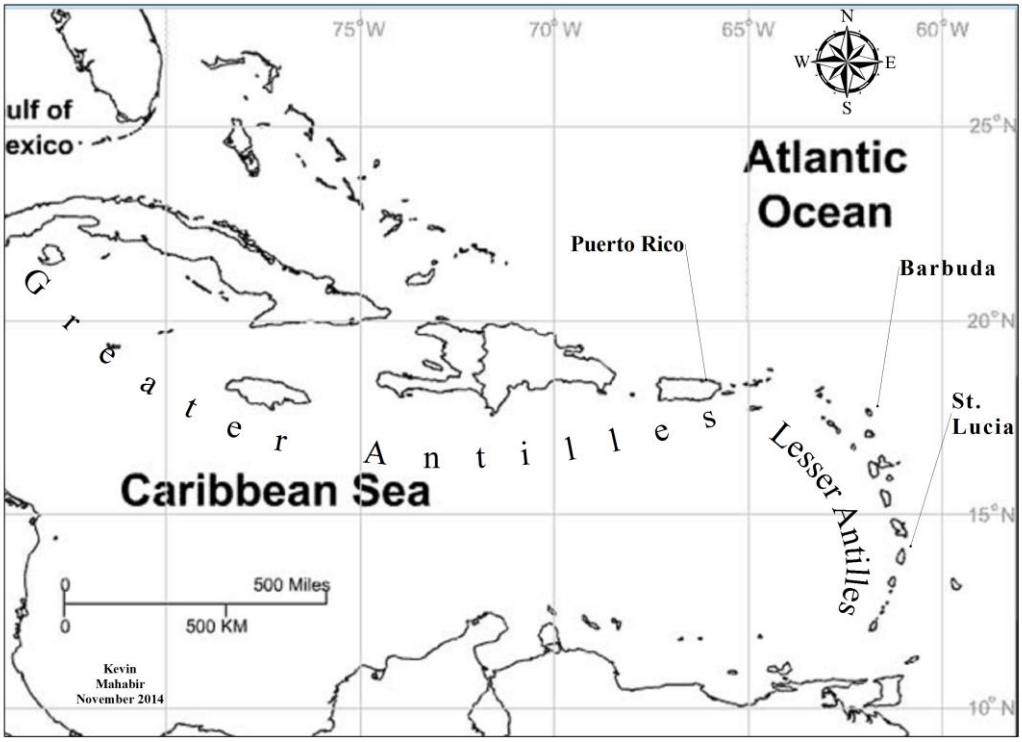

Figure 1.1: Regional geographic distribution of the now-endemic *Setophaga* warbler species; showing the Antillean single-island ranges.

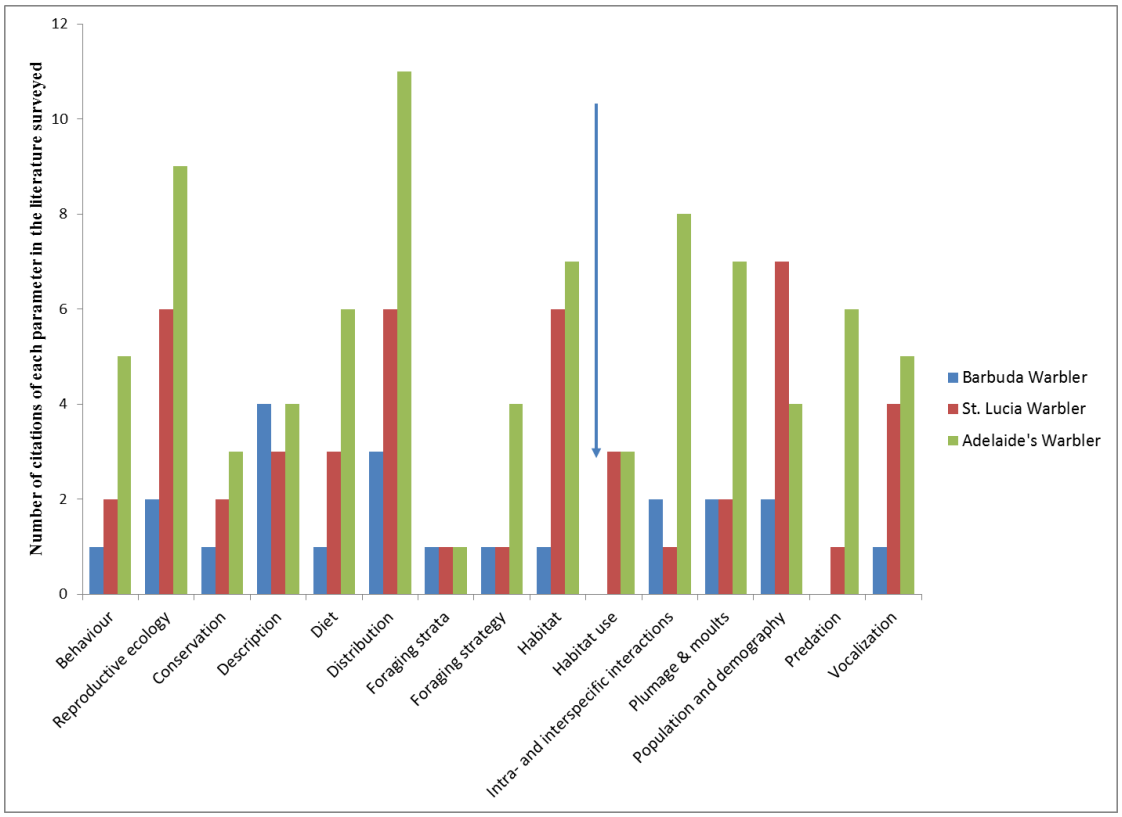

Figure 1.2: Number of papers on biological variables measured in the Barbuda (*Setophaga subita*), St. Lucia (*S. delicata*) and Adelaide's Warblers (*S. adelaidae*).

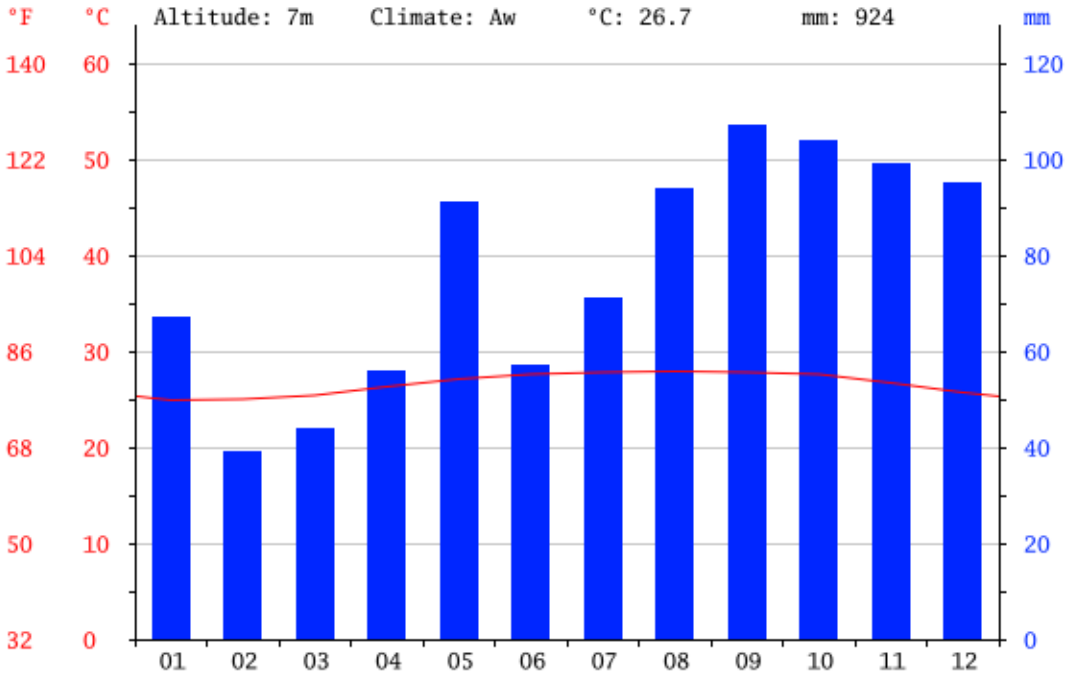

Figure 1.3: Illustration of annual rainfall and temperature pattern (from McSweeney *et al*. 2012)

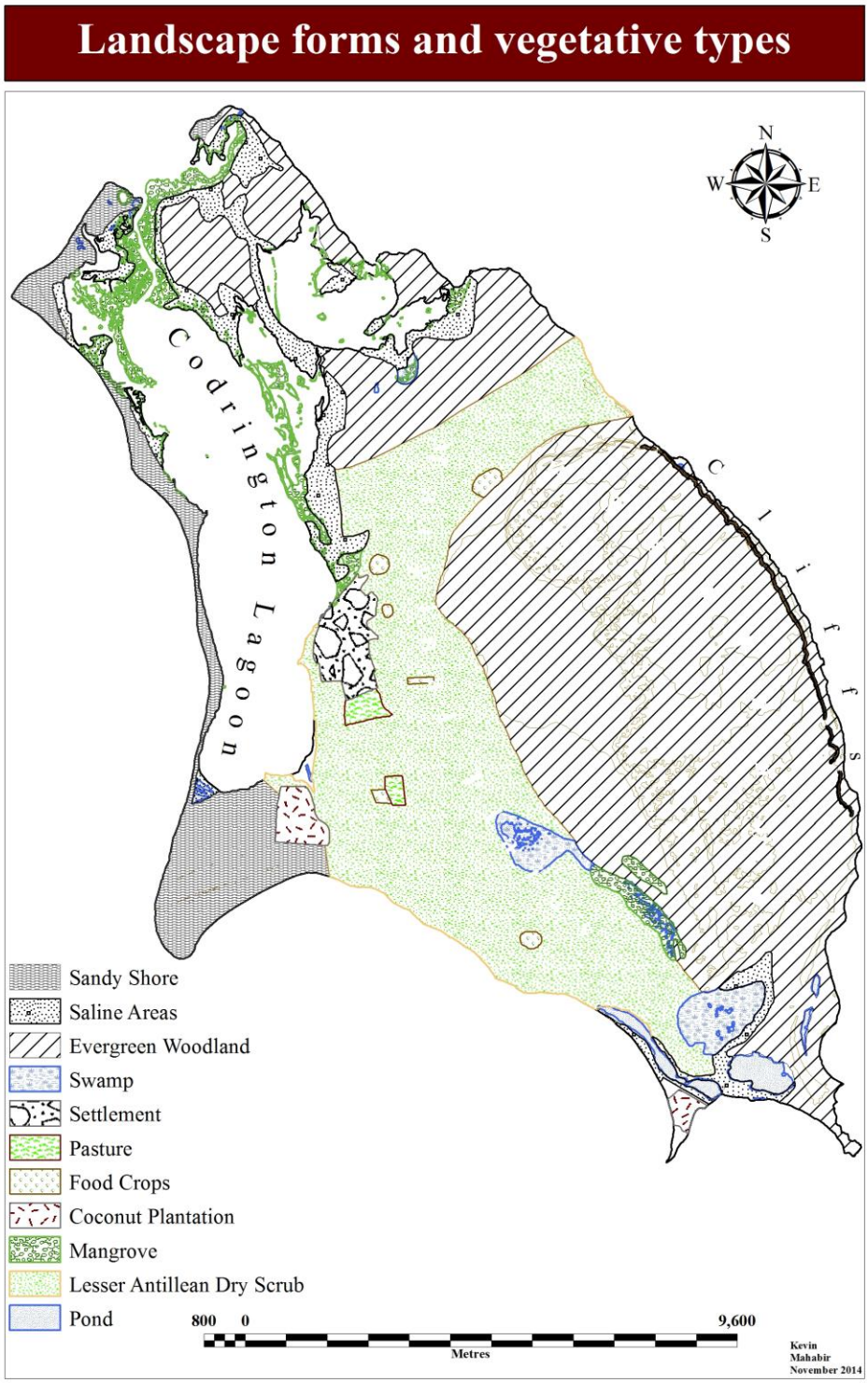

Figure 1.4: Physical map of Barbuda showing distributions of landscape forms and vegetation types.

Barbuda Warbler (***Setophaga subita***)	**St. Lucia Warbler** (***Setophaga delicata***)	**Adelaide's Warbler** (***Setophaga adelaidae***)
Xeric scrub Dry deciduous forest Forest edge Developed areas, Codrington Village Mangroves (uncommon) Dense low coastal vegetation (uncommon) Forest understory	Deciduous seasonal forest Semi-evergreen (lowland) seasonal forest Humid forests Second growth forest Undisturbed forest Forest understory Tree canopies (uncommon)	Dry deciduous forest (abundant) Dry limestone forest (abundant) Moist limestone forest Dense second growth forest Low dry scrub Developed areas, San Juan Forest understory

Table 1.1: Distribution of the Barbuda, St. Lucia and Adelaide's Warblers in vegetation types across Barbuda, St. Lucia and Puerto Rico, as described in Cornell Lab of Ornithology Neotropical Birds Online (Toms 2010a, b; Diamond 2011)

CHAPTER 2

GENERAL METHODS

Introduction

In counting landbirds the choice of method should be influenced typically, but not exclusively, by the focal species and the landscape (Wunderle 1994; Bibby *et al*. 2000). Some features on Barbuda facilitate some methods better than others. The point-count method (used on Barbuda) is preferred by ornithologists when identification of bird habitat attributes is needed. Point-counts use a fixed duration, allowing habitat features to be associated with the occurrence of a species more effectively than other methods (Bibby *et al*. 2000).

The interior Barbudan landscape, featuring the characteristically impenetrable Highland and xerophytic vegetation, described previously, is severely fragmented from feral livestock grazing. Winding lanes formed in such a manner provide much of the operable access, and so straight line-transects could rarely be accomplished. The line-transect sampling method has the additional disadvantage of a moving observer (unlike the stationary observer conducting a point-count), who may flush birds from the sample area before numbers are recorded, and may not be effective in detecting shy or stationary birds.

The Barbudan landscape is such that much of the vegetation is less than 5m high, which seemingly influences the flying height of many passerine Barbudan landbirds. Mist-netting effectively captures these species for close-up inspection, thus avoiding errors in recordings from human-observer census techniques; and colour-banding uniquely identifies each individual that can be seen with binoculars in the field. Regular

observations and re-captures of banded individuals can yield information on dispersal, territoriality, survivorship and recruitment of young into breeding populations. It is also used consistently and reliably to obtain demographic data on understorey passerine birds.

Measuring the reproductive condition, moult pattern, age and sex of birds in the hand, from mist-netting, and observations of colour-banded individuals are sufficient to estimate species' seasonality in this project. Several aspects of both warblers' life history, reproductive and behavioural ecology are poorly known and the extent of knowledge can be expanded through examining birds in the hand. Furthermore, future monitoring using mist-netting and banding will assist in long-term evaluation of the status of the population.

Design

Sampling schedule

Four visits to Barbuda were made to sample each season as equally as possible. Netting and point-counting were conducted during the peak of avian activity on dates shown in Table 2.1; (generally 05:30-10:00 for point-counts, 06:00-11:00 for mist-netting, in non-rainy weather). Coordinates and distances were measured with a Garmin GPSMAP 62s unit, based on the WGS 1984 datum. Surveys, netting and banding were done with the permission of the Barbuda Council and under Banding Permit No. 10480 (Environment Canada) to A.W. Diamond.

Point-count sample-stations

A digital base map of the island of Barbuda was constructed using ArcGIS® software, with a systematic grid overlay dividing the island into 8 large sampling regions. The overall design involved sampling each region at least once on each visit to the island.

A distribution of point-count sample stations (each 0.28 ha) within each region was generated by a constrained randomisation process in ArcGIS 10.2, and overlaid as a single layer on the whole base map (Figure 2.1). Stations were randomly sited, but if any two were within 400 m (Huff *et al*. 2000) of each other, a new set of coordinates was randomly generated for one of them. This reduced the risk of detecting the same bird again at the next point count.

Because many sample-stations were located in impenetrable thickets of thorny scrub, the inaccessible stations were relocated to the nearest accessible location, which were mostly along lanes formed by livestock browsing and grazing. This compromise offset the sample-station centre by no more than 5 m; and because of the severity of fragmentation from grazing and the resulting abundance of lanes, it is assumed that no micro-habitat was missed at those sample-stations.

Selection of a region (one of eight in the grid overlay, Figure 2.1) to be sampled was made using a random number table. The first point sampled per region was often the pre-mapped coordinate closest to the road (or vehicle drop-off point). The next closest pre-mapped point was then sampled, or a new one was created after walking for at least 400 m along the lane, if there were no other pre-mapped coordinates within 400 m of the previous point. Each sampling region and the component sample-points were selected in this way on each point-count sampling-day; however a region was not sampled twice in the same field-trip.

Attempts were made to sample each region in each season in a way that maximises equal spatial and temporal sampling, reducing the risk of confounding spatial

with temporal variation. I applied a spatially stratified approach, with points every 400 m, adjusted as necessary by ease of access.

Diamond's (1973) study on St. Lucia suggested that inter-specific interaction between closely related *Setophaga* (then *Dendroica*) warblers there may influence their local habitat distribution. Consequently, I have included here each warbler species as a possible explanatory variable for the occurrence of the other.

The numbers of Barbuda and Yellow Warblers were recorded at each point, as well as physical environmental attributes such as landform, the presence and species of plants fruiting and in flower, and distance from freshwater (Chapter 3, Table 3.1). Plant identification and details of phenology were referenced from Pratt *et al*. (2009). Of the 224 point-count sample-stations, each 0.28 ha (~ 63 ha to be sampled, ~ 0.44% of Barbuda's accessible area), 76 were situated in the marginal plains of the island, with often impassable dense and thorny vegetation of the *Haematoxoglon* or *Acacia* genus; 49 in the Highlands where mixed deciduous woodland is dense; 38 in or adjacent to mangrove growth (one or a combination of *Avicennia germinans* and *Rhizophora mangle*, or the more drought-resistant *Conocarpus erectus* or *Laguncularia racemosa*); 28 in developed areas in and around Codrington Village where exotic vegetation and domestic gardens are prominent; 17 at the inshore and mudflat zones around the island, where the vegetation is invariably windblown and of short stature or creeping (such as *Coccoloba* or *Ipomoea*); and 16 on the coast, featuring maritime scrub and some sparse mangrove growth (Table 2.2).

Mist-netting stations

Mist-netting was conducted during the same sampling trips as the point-counts, and was used to capture both species of warbler for measurement of species, age, sex, and breeding or moulting activity, and for colour-banding. Mist-netting stations were established opportunistically ("active" mist-netting stations) to capture Barbuda and Yellow Warblers; that is, stations were set up at sites of localised Barbuda or Yellow Warbler activity or singing. Observations made during or between point-count sessions were used as cues for return trips to the area for mist-netting.

Mist-netting stations at the lowland sites featured vegetation that was mostly scrubby and xerophytic, usually with one or two thorny species, 1-3 m in height. A few mist-netting sessions were conducted near mangrove growth, a few at inshore areas, and one on the north coast at Two Foot Bay near a freshwater pond. All mist-netting days were dry and sunny. In the months of sampling there were a few plants in flower at point-count and mist-netting stations; fruit was uncommon and usually consisted of small berries.

Chapter 3 presents the details of the specific procedure used to fulfil the objective of warbler distribution and habitat associations. Also presented is the analysis that will be performed on the data collected according to these specific procedures. Global and reduced models are presented as attempts to explain Barbuda and Yellow Warbler occurrences with respect to the presence of physical habitat influences. The reliability of these models to explain warbler presence is also discussed.

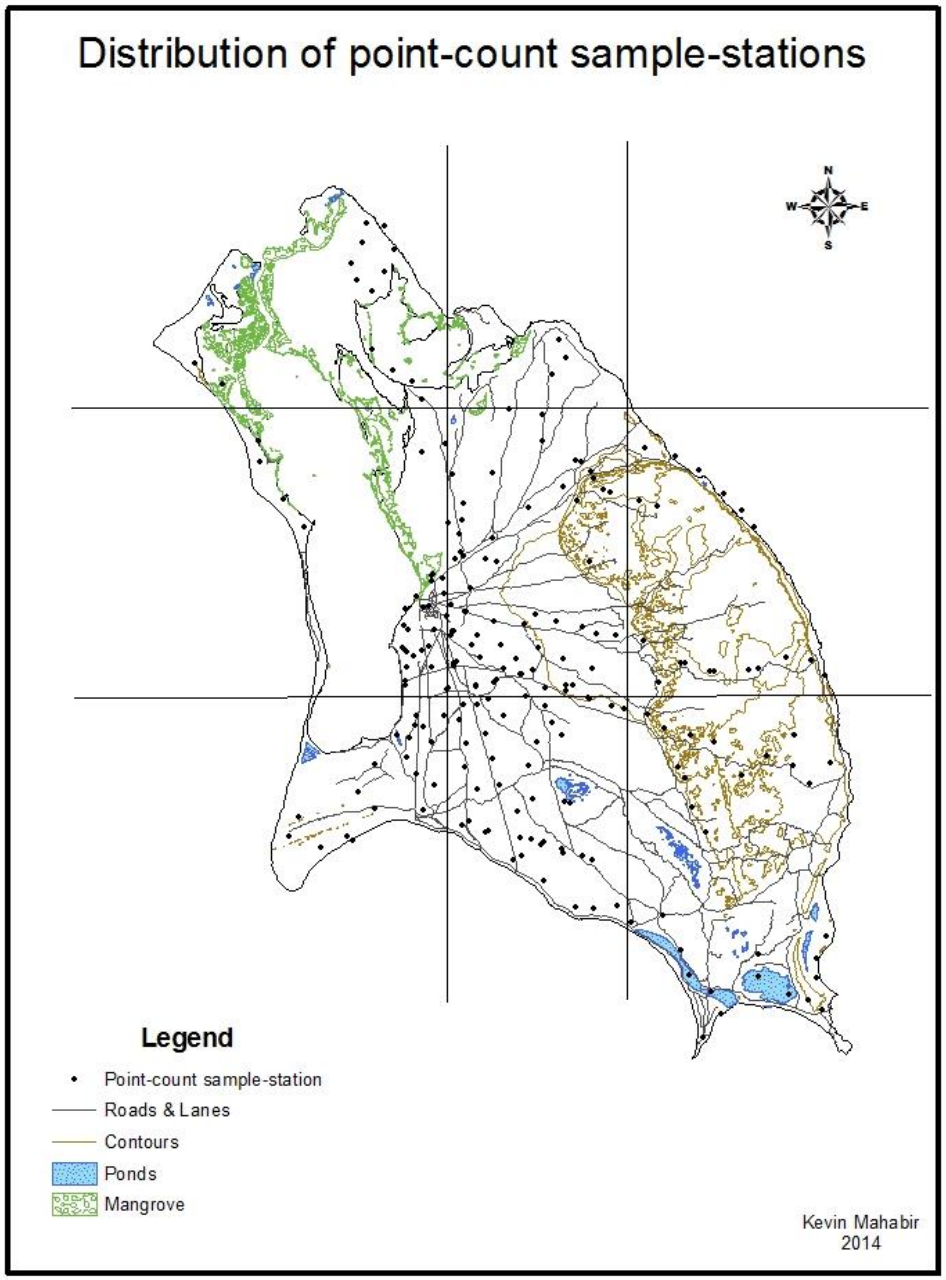

Figure 2.1**:** A random distribution of 224 point-count sample stations was generated across an 8-sample-region grid-overlay.

Table 2.1: Log of point-count and mist-netting sessions. On Barbuda, wet season – May to October; dry season – November to April.

Trip number	Dates	Season	Point-count sampling sessions	Mist-netting sessions
1	3 – 29 June, 2013	Summer	46	8
2	3 – 29 September, 2013	Autumn	50	8
3	1 February – 3 March, 2014	Winter	67	7
4	3 May – 4 June, 2014	Spring	61	6

Table 2.2: Distribution of point-count sample-stations across major landscape forms

Landscape	Plains	Highlands	Wetlands	Inshore	Developed	Coasts
# of points sampled	76	49	38	17	28	16
% of landscape sampled	5.5	2.3	1.5	1.4	2.6	2.8

CHAPTER 3

DISTRIBUTION AND HABITAT ATTRIBUTES OF BARBUDA AND YELLOW WARBLERS ON BARBUDA

In characterising the habitats and distribution used by both Barbuda and Yellow Warblers, island-wide surveys of warbler presence and associated components of habitats were performed. Point-count data, collected in a stratified random framework, were used in analyses to help with these characterisations.

Procedure

Field Sampling

224 fixed-radius point-counts (Bibby *et al*. 2000) were used to record the presence and numbers of Barbuda and Yellow Warblers detected aurally and visually across the island. Design of the sampling framework was discussed in the previous chapter, which includes selection of sample regions of the island and sample-stations to be used.

At the sample-station data were recorded first that could be collected only while standing still, e.g., location, weather, visibility (this allowed the birds some time to adjust after initial disturbance). Location and distances were recorded using a GPSMAP62s unit (WGS1984 datum). Weather was recorded according to my judgement, categorised by Sunny; Drizzle; Constant rain; Heavy rain. Overhead cloud cover (0-33%; 33-66%; 66-100%) at the sample-station was also recorded according to my visual estimate. Visibility estimates of “Good” were subjected to my certain ability to visually detect a warbler in the sample station on a sunny day. “Medium” and “Poor” visibility was recorded when

light was low (such as an overcast early morning), or when drizzling, thus obscured vision (studies of warbler detectability in different environmental conditions and habitats are necessary to complement presence/absence data). Other attributes were ascribed to each sample station according to pre-selected variables (Table 3.1) (DeGraaf *et al*. 1998). Canopy coverage was recorded as my visual estimate of the fraction of the sky not obscured by foliage. Canopy height was easily estimated without instruments, and recorded as <5m, 6-10m, 11-20m. Foliage density (0-25%; 25-50%; 50-75%; 75-100%) at a point was recorded as my estimate of leaf-area coverage at the vegetation level where warblers are seen to forage, rest, or interact. Because Barbuda and Yellow Warbler response to human disturbance on Barbuda is not known, I chose to record "Anthropogenic development" at the point-count as "nearby buildings or roads; or recent cutting or clearing of vegetation." Vegetation types were recorded based on my discretion of >50% dominance of certain plant types at the sample-station. Exotic vegetation was recorded when ornamental plants were observed; Grassland was recorded when there was a dominant expanse of continuous grass and no trees; a Pasture was recorded when the Grassland supports designated animal grazing; Highland mixed species was recorded in the Highlands when there was no discernible dominant plant species; Mangrove was recorded when there was a dominance of mangrove plants (easily identified red, white, black, and button mangrove plants); Maritime scrub was recorded when plants were low and windblown, often with stiff woody bases and softer branches; Mixed scrubland was recorded when I discerned a mixture of scrub species with no obvious dominant species; Thorny scrubland was recorded when >50% of the vegetation comprised thorny species.

The count began after these data were recorded, and as much as possible, the presence of a warbler was recorded immediately upon detection; or it was assumed that the birds were detected at their initial location (Buckland *et al*. 2008). From the start of the count, for five minutes, the numbers of Barbuda and Yellow Warblers seen or heard within 30m of the point were recorded (Figure 3.1 & 3.2); beyond 30m, warblers detected were registered as "*present*" (Bibby *et al*. 2000). Warblers flying directly overhead were excluded from the count if judged not to be associated with the habitat. Overhead warbler flight that is fixed (such as a straight line), and above the tallest emergent tree at the sample station, was judged to be an independent fly-over (Huff *et al*. 2000; Hanni *et al*. 2008). In randomly generating the sample-point distribution, I specified that points were at least 400m apart. In these ways I attempted to avoid double-counting an individual, but I cannot be sure if I was completely successful. Additionally, analyses used presence/absence data, not numbers of individuals, so results are not affected.

After the count, photographs of the sample-station and its surroundings were taken. From these photographs, dominant vegetation species were identified (Pratt *et al*. 2009). Within the sample station, plant species that were fruiting or in flower at the point were recorded (Bibby *et al*. 2000; Frampton *et al*. 2001; Jain *et al*. 2010).

The geographic location of each sampled point-count station was recorded in UTM coordinates, and warbler presence at these points was mapped using ArcGIS® software.

Data Analysis

A Pearson's x^2 (chi-squared) test, or goodness-of-fit test, calculates how likely the observed warbler distribution is due to chance, and is used here to test if Barbuda and

Yellow Warblers are distributed independently of each other. Tests for significant differences in warbler presence across point counts were done using the Kruskal-Wallis test on multiple samples categorised by landscape form. Tests were performed on presence/absence data at all 224 point-count sample stations. An alpha level of 0.05 was used to assess statistical significance.

Multivariate logistic regression modelling of measured habitat attributes, performed in R (2015 ver. 3.2.2 (2015-08-14)) was used to explain the presence of the Barbuda and Yellow Warblers. The log odds of the presence of a Barbuda Warbler are modelled as a linear combination of the habitat attributes. These attributes are of mixed data types; categorical variables are converted in R into usable integer representations. I used the function **as.factor,** which stores categorical variables as integers, but maintains associations with the original character values to be displayed when the factor is returned after processing. Levels of a variable are also re-coded as factors to be used in processing. For instance, the program treats the levels of "Landscape" as factors, but they are un-ordered, such that "Wetlands," e.g., is discrete from "Plains," instead of "Wetlands" < "Plains" or "Wetlands" > "Plains."

A Generalised Linear Model (GLM) function in R is used to fit the data to logistic regression models (terms added sequentially), **Barbuda Warbler Presence** ~ Canopy coverage + Canopy height + Landscape form (Developed areas; Highland; Inshore areas; Plains; Wetlands) + Vegetation type (Exotic; Grassland; Highland mixed species; Mangrove; Maritime scrub; Mixed scrubland; Pasture; Thorny scrubland) + Vegetative strata + Foliage density + Anthropogenic development + Dominant plant species + Temperature + Distance from freshwater + Yellow Warbler Presence; and

Yellow Warbler Presence ~ Canopy coverage + Canopy height + Landscape form (Developed areas; Highland; Inshore areas; Plains; Wetlands) + Vegetation type (Exotic; Grassland; Highland mixed species; Mangrove; Maritime scrub; Mixed scrubland; Pasture; Thorny scrubland) + Vegetative strata + Foliage density + Anthropogenic development + Dominant plant species + Temperature + Distance from freshwater + Barbuda Warbler Presence

where each variable affects the model's suitability. The above generalised model is not an "ideal" model, but rather an approximation; it is reasonable to expect that some variables can contribute more information to the model than others (Hand and Vinciotti 2003).

In the linear models, collinearity in explanatory variables increases the standard errors of the model and forces the coefficients towards zero, making the measured attribute erroneously insignificant. Thus, lower collinearity indicates that the coefficients obtained may be more significant to the model than they would otherwise have been. In this study, the low measures obtained in the correlation matrix do not require removing or adjusting pairs of correlated variables in the global models. I considered variables to be collinear when $r > 0.6$ (Evans 1996).

The Akaike Information Criterion (AIC) (Akaike 1974) method ranks the different models and the GLM package in R reduces the generalised (full) model to a group of other possible models with different combinations of variables, ranked by AIC score. The resultant models reflect degrees of loss of information in relation to the generalised model. In assessing overall performance of the models, that is, to measure how closely the models fit the observed data, goodness of fit of each full model is calculated by likelihood ratio tests on each full model via analyses of variances. The full

models are compared to null models (full models restricted to models each with only an intercept term: no explanatory variables; i.e., restricted by a null hypothesis that the coefficients of each of the variables are equal to zero). Comparison of models is facilitated by the measure Delta AIC, which is a measure relative to the 'best' model (the model with the lowest AIC score). Burnham and Anderson (2002) provided guidelines, suggesting that an AIC score between 2 and 4 suggests a moderately likely explanation of the outcome. Akaike weights provide the Delta AIC measure on a scale of 1 and evidence ratios reflect how better the best model is than any other specified model. The intent is to illustrate the habitat features of (presumed) importance to both the Barbuda and Yellow Warblers, and describe their distribution pattern relative to the mapped habitat features.

Results

Detections of Barbuda and Yellow Warblers per field trip are illustrated in Table 3.2. The number of each species observed within 30 m of the sample-station's centre is presented as a measure of relative abundance. The number of point-count sample-stations in which each species was recorded is given in parentheses, as well as the time spent counting per field-trip. Mutual detections are presented as the number of point-counts where both species were detected, at all distances.

Low coincidences of both warbler species during point-counts (Table 3.2) suggest that the two species may be negatively associated with each other. Per month calculations estimate that the distributions of Barbuda and Yellow Warblers are not random, in relation to each other, or, they are not distributed independently of each other (Table 3.3). Summing values for all months, $x^2 = 46.32$, $p < 0.0005$, this verifies that Barbuda and Yellow Warblers are distributed in negative association to each other.

Figures 3.1 & 3.2 illustrate the distribution of each warbler species on maps of major landforms of the island, combining all surveys. Broad landscape forms are included to give a visual perspective of relative habitat use. They are the Highlands, the Plains, Inshore areas, Coast, and Wetlands including ponds, swamps, low-lying moist/wet freshwater areas, mudflats, and wherever there is mangrove growth. The scale of habitat/landscape presented is an indication of broad habitat selection of the warbler species. These illustrations are used to guide finer statistical analyses of habitat selection, thus assisting in final species distribution models.

A Kruskal-Wallis test showed no significant differences in Barbuda Warbler presence across landscape form ($\mathbf{H_{adjusted}}$ = 8.621; **d.f.** = 5; $\boldsymbol{p}$ = 0.125); Yellow Warblers, however, showed a relatively remarkable difference in their occupancy of different landscape forms ($\mathbf{H_{adjusted}}$ = 23.617; **d.f.** = 5; $\boldsymbol{p}$ = 0.0003). Because of this significant difference, post-hoc pair-wise multiple comparison Dunn's test was conducted to identify between which pairs of groups were there differences. It showed greatest differences in Yellow Warbler presence between Wetlands & Plains ($\boldsymbol{p}$ = 0.0007), Wetlands & Highlands ($\boldsymbol{p}$ = 0.004), and Wetlands & Coasts ($\boldsymbol{p}$ = 0.004).

Although figures show high densities of warbler detections in the plains area where there is dry low scrub, there was also a disproportional amount of effort spent in those areas, certainly inflating relative abundances with respect to sampling equity. However, enough samples and incidental observations were taken elsewhere to conclude that warbler densities are indeed high in the drier low thorny scrub of the plains (0.41 BWs, 0.32 YWs per point-count); Yellow Warblers seem to be distributed more densely

than the Barbuda Warblers across most landscape forms, except the marginal plains (Tables 3.4 and 3.5).

In the correlation matrix (Table 3.6), the strength of association of the explanatory variables, +/- 0.3, reflects associations that are low enough – or do not significantly correlate – to allow the pairs of variables to remain in the generalised models for further analyses.

Results of goodness-of-fit tests are presented in Tables 3.7 (Barbuda Warbler) and 3.8 (Yellow Warbler). Table 3.7 shows a likelihood ratio test statistic of 94.89, with a p-value of 0.051. Given the calculated p-value here, the relationship merits further investigation.

Table 3.8 shows a likelihood ratio test statistic of 123.36, with a p-value of 0.0003. The calculated p-value here suggests that the null hypothesis can be reliably rejected. Here the full model of Yellow Warbler presence also fits better than the null.

From R analysis, models and calculated values of AIC, Delta AIC, AIC Weights and Evidence Ratios are presented in Tables 3.9 a & b.

A stepwise AIC method reduced global models to more parsimonious suites of explanatory variables. These reduced models with a Delta-AIC score < 4 (Mazerolle 2004; Burnham and Anderson 2002) are presented in Table 3.9. Barbuda Warbler presence was apparently influenced by Yellow Warbler presence, and changes in canopy height and temperature; and Yellow Warbler presence was influenced by landscape form, vegetation, temperature and, to a much lesser extent, canopy height.

Modeling multivariate habitat data with logistic regression assumes that the logit transformation of the presence of a warbler has a linear relationship with the explanatory

variables. The variables chosen to be measured were selected based on published assessments (Bibby *et al*. 2000; Frampton *et al*. 2001; Jain *et al*. 2010).

Global (generalised) models:

I first assessed the suitability of the full models before attempting to reduce them. The likelihood ratio test compares the log likelihoods of the full model and the null. This is applied to both the Barbuda Warbler model and the Yellow Warbler model. The full suite of measured variables explains the Yellow Warbler's occurrence better than the same variables explain the Barbuda Warbler's occurrence. The focus here is which of the reduced models for each warbler species is most parsimonious.

Stepwise regression using AIC:

The stepwise regression process begins with the fitted full model, whose likelihood of parsimoniously explaining the presence of either warbler species is extremely low. Table 3.9 show the span of Delta AIC values and how much the global model is outside the range of Burnham and Anderson's (2002) "more likely" models.

I used a stepwise reverse regression method which obtains from the generalised models a few simpler ones – models which contain less than the full suite of measured variables. The method sifts through the many measured variables of each, successively removing variables, fine-tuning the models based on the variables' estimated coefficients.

Customarily, models with a lower AIC score are more reliable than those with higher scores. The measure relied upon here follows Mazerolle (2004), which proposes Delta AIC – a measure of each model relative to the one with the lowest AIC score: AICi – min AIC, where AICi is the AIC value for model i. Mazerolle (op. cit.) suggests that a Delta AIC value less than 2 conveys substantial evidence for the model, while Burnham

and Anderson (2002) suggest that a value between 2-4 is moderately supportive, and a value greater than 4 indicates that the model is "very unlikely."

The reduced models according to the conventionally parsimonious criteria above are

Barbuda Warbler Presence ~ Canopy Height

and

Yellow Warbler Presence ~ Landscape form

Examination of model Barbuda Warbler Presence (from Table 3.9a and R analysis) shows the best model contains just Canopy Height, and the second best contains Yellow Warbler presence, Canopy height and Temperature (in models with Delta AIC < 4); and between them both they have a combined Akaike weight of 0.64. Adding the influence of anthropogenic development increases the overall Akaike weight by only 0.6. Adding variables like this explains more of the presence of Barbuda Warblers than if canopy height alone is considered, but the strengths of these models are low. These models also cross the AIC < 4 threshold, so they are not considered as significant.

The effect of Landscape form (presence of wetlands) alone is contained in the best model and has an Akaike weight of 0.45; combining vegetation (absence of "highland mixed species" association, presence of mangrove growth) with the top model gives a combined Akaike weight of 0.72. Adding variables up to model # 5 crosses the AIC < 4 threshold, and so is not considered a significant contributor to Yellow Warbler Presence.

Discussion

The AIC stepwise reduction process calculates how much each added variable contributes to the overall probability that the model is the best among models. Canopy height, the strongest influence (Akaike weight 0.49) on the probability of Barbuda Warbler occurrence, is not very varied on Barbuda; landscape forms are expansive and the vegetation generally homogenous. Still, Barbuda Warblers were found more often in the higher canopies, in the range of 5-10 m. These trees are rarely the thorny species which dominate most of the plains (where both warblers occur in abundance), but rather *Tabebuia heterophylla* and *Bursera simaruba*, as well as some of the exotic and introduced species in the developed areas. Figure 3.3 shows prominent co-occurrence of high-canopied trees and warbler (either species) presence, but a close inspection will show the effect of Barbuda Warblers' avoidance of Yellow Warblers within the distribution of high-canopied trees.

Adding the influence of Yellow Warbler presence and temperature increases the "best-model" Akaike weight score to 0.64 (Table 3.9a). The influence of temperature cannot be realistically interpreted given the modelling results of these data. Temperature probably varies more during a sampling period, and between months, than between habitats. Studies should be designed to standardise sampling times, as the effect of temperature will be evident if the temperature varies during the sampling session. Yellow Warblers persist as a negative influence in the Barbuda Warbler Presence stepwise regression reductive modelling. In reality, this reflects low co-incidences of both warbler species at a sample station. The effect of Yellow Warblers on Barbuda Warbler presence can be appreciated by considering their respective densities of co-occurrence in wetlands

(Yellow Warblers: 0.71 birds per point-count; S.E. 0.14; Barbuda Warblers: 0.24 birds per point-count; S.E. 0.07).

Including variables beyond these discussed move the model past the acceptable thresholds from Burnham and Anderson (2002).

Landscape form was a persistent model component for presence of Yellow Warbler (Table 3.9b). The wetland landforms (within which is "wetland vegetation" according to this survey) contribute more significantly to the presence of the Yellow Warbler than the other landforms surveyed. The presence of mangrove growth on the island is prominent at lagoon edge and ponds; here the areas are considerably wet underfoot, but the prominence of Yellow Warblers in the driest zones of these wet areas (where White Mangrove appears to dominate) suggests fine-scale resource selection occurs within general mangrove growth (White, Black, Red, and Button). These wet areas are evident on the maps in this thesis, and include moist mangrove growth, and wet vegetation around permanent ponds and seasonally flooded areas, as well as on the perimeter of the lagoon. The Yellow Warblers' presence in mangrove growth and wetlands are expected given this study's data, but their avoidance of the highland species is yet unclear. Their presence is not apparently affected by Barbuda Warbler presence, so Yellow Warblers' avoidance of this vegetative association is most likely not due to Barbuda Warblers' affinity for it. The thorny species of the plains, *Haematoxylon campechianuum*, *Acacia tortuosa* and *A. macracantha* seem to support the Yellow Warbler's daily movements, as observed during and between point counts.

Landscape and vegetation contribute to a combined Akaike weight of 0.72. As discussed above, temperature was deemed inadmissible in these analyses, so it is omitted

from considerations here. Canopy height barely adds any strength to the model's explanatory power, so this aspect of the vegetation is not a reliable contributor to the Yellow Warbler's presence.

Further investigation is needed to better understand which selected resource (or pressure) contributes to the Yellow Warbler distribution.

The presence of a species in a habitat seems sufficient to state that there exists within that habitat a suite of resources selected in some unspecified proportion to the resource's availability. However, a species' presence cannot indicate how much the resource is preferred. Even estimates of abundance lack conclusiveness among researchers as indicators of habitat suitability (Marra and Holmes 2001), especially so since the suitability of habitat includes the dynamic effect of interspecific interactions.

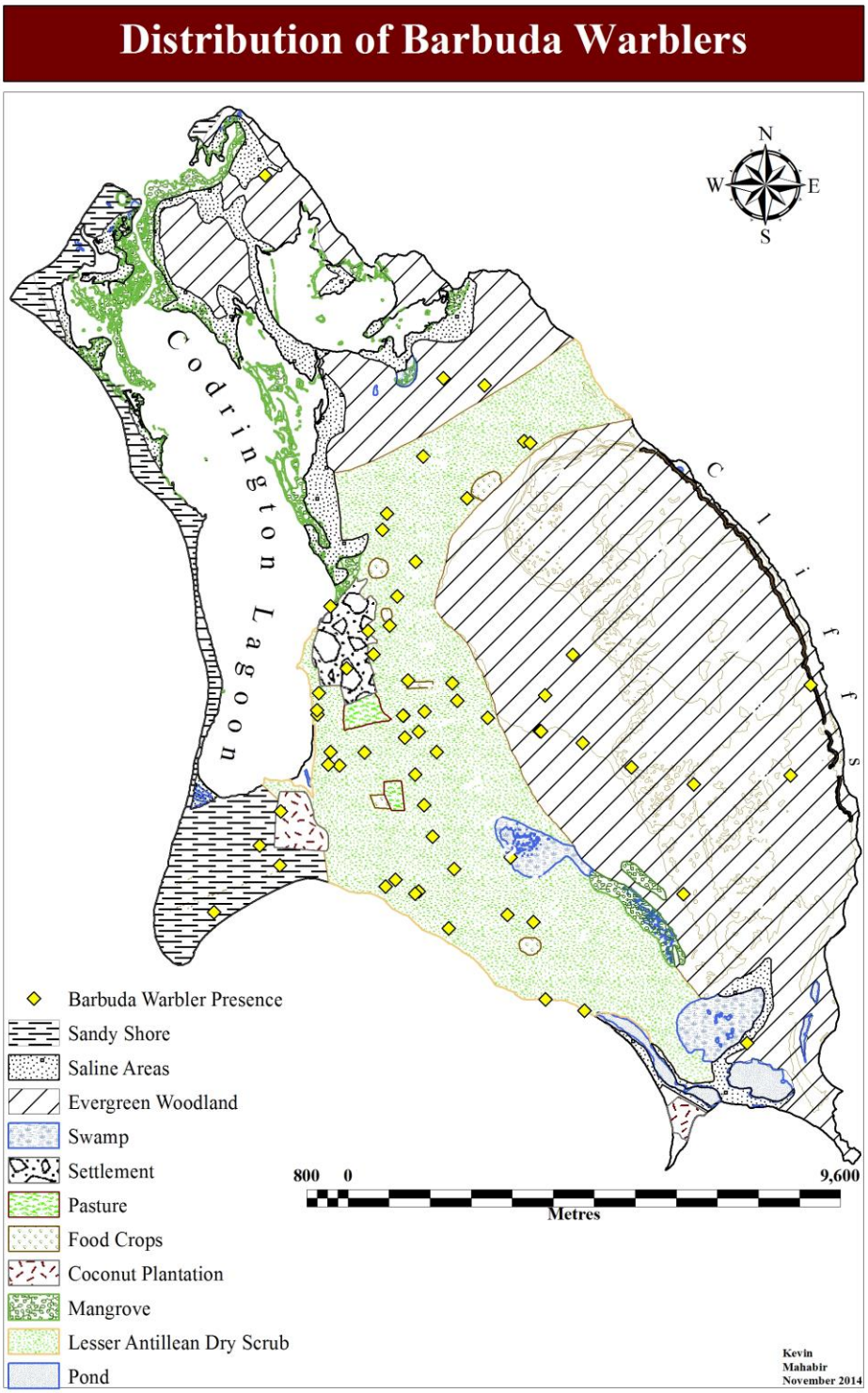

Figure 3.1: Distribution of Barbuda Warbler detections at 64 point-count sample-station across the island.

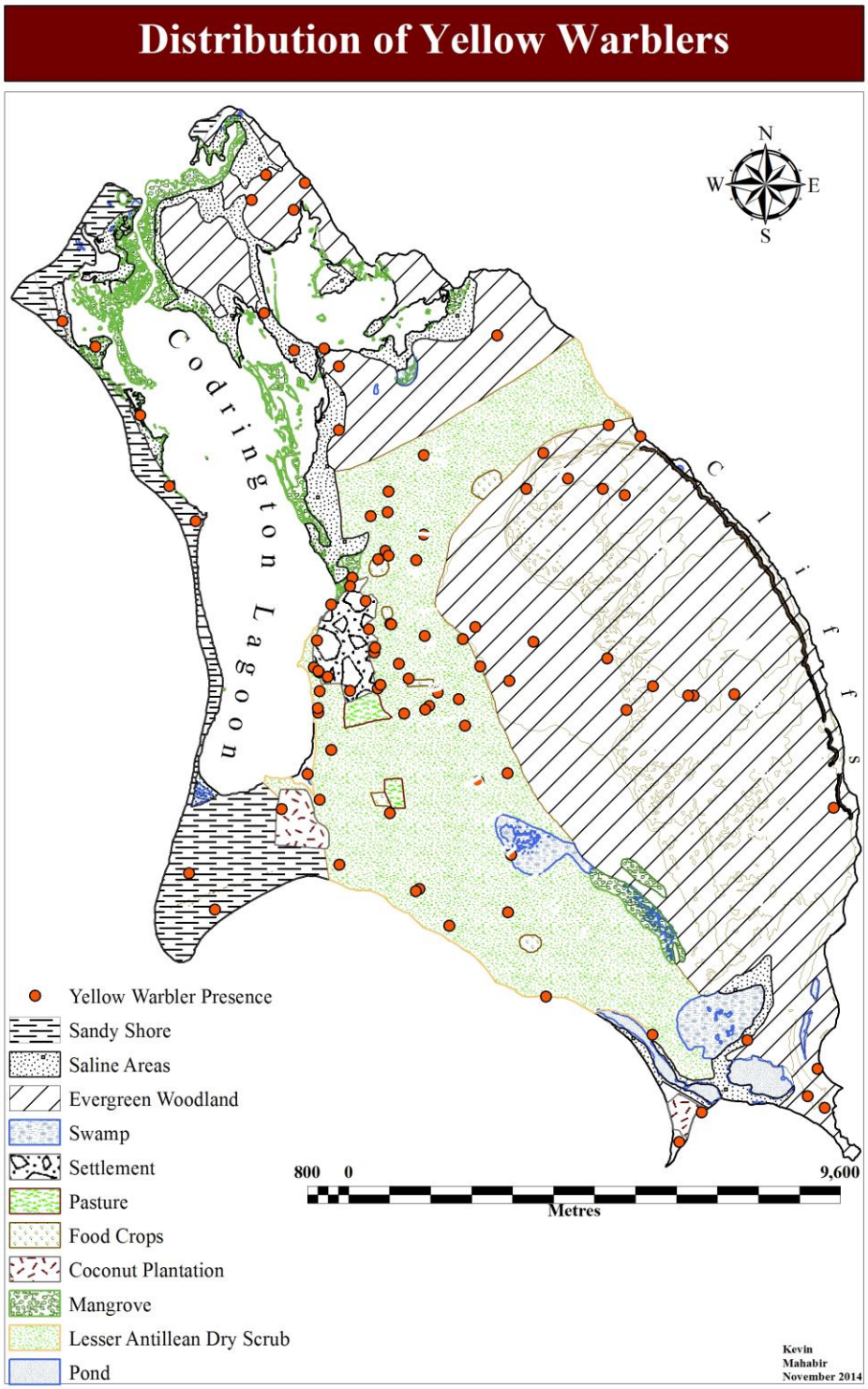

Figure 3.2: Distribution of Yellow Warbler detections at 95 point-count sample-stations across the island.

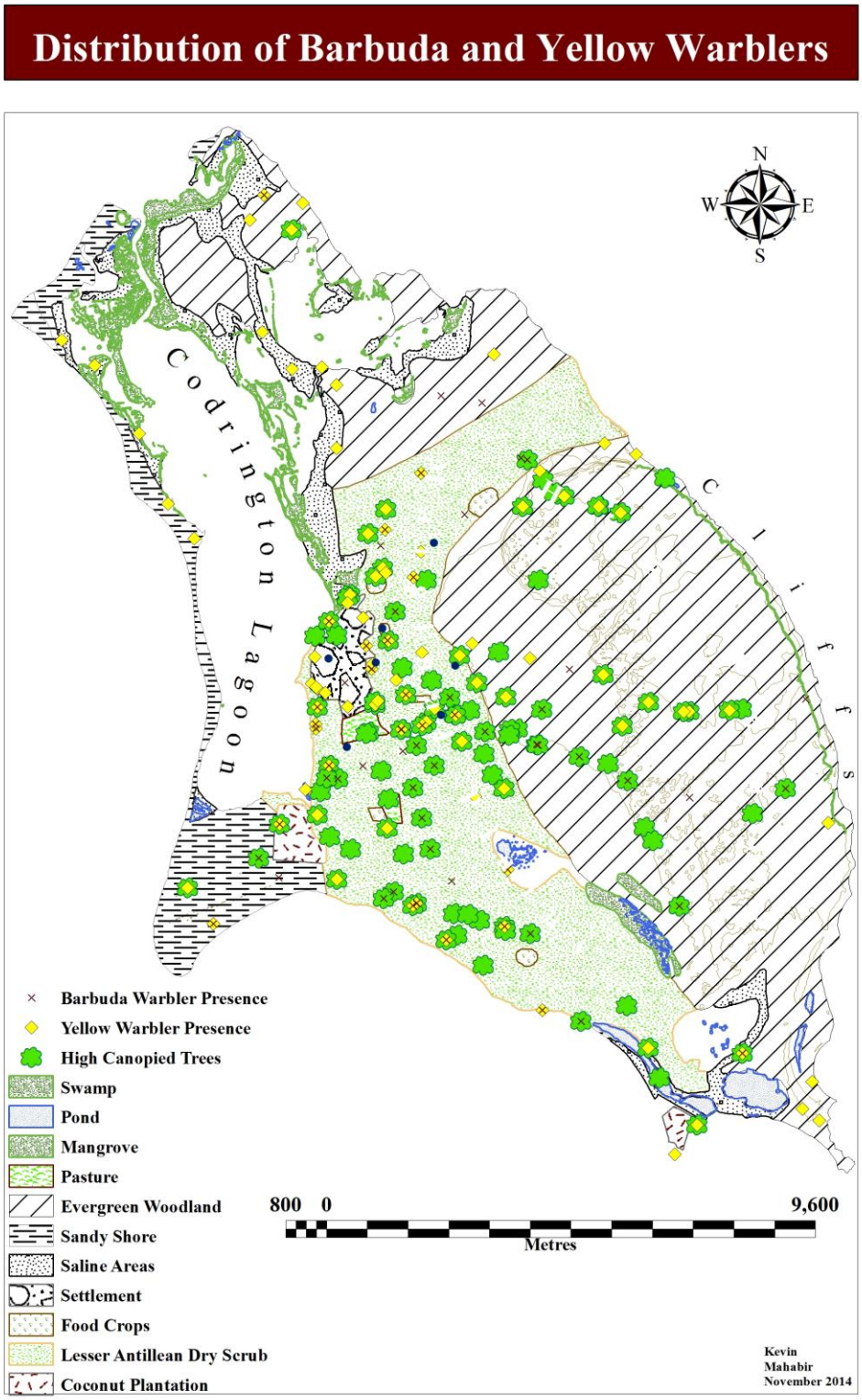

Figure 3.3: Distribution of Barbuda and Yellow Warblers show low co-incidence, and their use of fragments of stands 10 – 20 m high.

Table 3.1: Measured variables and their attributes recorded at each point-count sample-station.

Attribute	Data	Description
Canopy Coverage	0-25%; 25-50%; 50-100%	Proportion covered by tree crowns
Landscape	Coast; Inshore; Lagoon/Wetland/Pond; Highland; Plains; Developed areas	Physical elements categorised into geophysically defined forms
Canopy Height	5-10m; 10-20m; 20-30m	Height of the highest portion of the tree crowns above ground level
Vegetation	Highland Mixed Species; Evergreen Woodland; Thorny Scrubland; Mixed Scrubland; Pasture; Mangrove; Maritime Scrub; Exotic	Plant assemblages that characterize the vegetation, each dominated by one or two definitive species
Vegetative Strata	Herbaceous Layer (<1m); Scrub Layer; Understorey; Canopy; Canopy/Herb layer (<1m); Canopy/Understorey; Mangrove Islands; Emergent	Classifies vertical layers of the vegetation
Foliage Density	0-25%; 25-50%; 50-75%; 75-100%	Estimation of leaf coverage in vegetation
Wind	Integer in km/hr	Wind speed
Temperature	Integer in degrees Celsius	Measured temperature
Anthropogenic development	Yes/no	Signs of human development visible from point-centre
Distance from freshwater	Integer in metres	Distance from point-count centre to nearest freshwater

Table 3.2: Detections per field trip; number of sample-points in which each species was recorded is given in parentheses. Table shows low co-incidence of both Barbuda and Yellow Warblers, considering the relatively high number of sample-points in which each species was detected without the other.

	June (260 min)	September (255 min)	February (335 min)	May (300 min)
Barbuda Warblers only	20 (15)	8 (6)	27 (23)	26 (20)
Yellow Warblers only	31 (17)	40 (27)	23 (18)	43 (33)
Both Barbuda & Yellow Warblers	(3)	(3)	(7)	(10)
No detections of either	(17)	(20)	(33)	(18)

Table 3.3: Results of Pearson's chi-squared test reject the null hypothesis - Barbuda and Yellow Warblers appear distributed in negative association with each other.

Month	**Calculated Chi-Squared**	**Probability level**
June	9.48	$0.001 < p < 0.01$
September	29.52	$p < 0.0005$
February	37.24	$p < 0.0005$
May	8.05	$0.0025 < p < 0.005$

Table 3.4: Number of Yellow Warblers & Barbuda Warblers (in parentheses) sampled per point per landscape form.

Landscape form	Mangrove growth	Highlands	Developed area	Inshore	Plains	Coast
# of birds per point	0.71 (0.24)	0.33 (0.22)	0.54 (0.29)	0.53 (0.12)	0.32 (0.41)	0.25 (0.19)
# of months surveyed	4	4	3	3	4	4
Standard error (of # of birds per point)	0.14 (0.07)	0.16 (0.09)	0.12 (0.02)	0.09 (0.05)	0.07 (0.12)	0.10 (0.11)

Table 3.5: Number of stations of Barbuda (in parentheses) and Yellow [in brackets] Warbler presence per broad landscape form. Number of sample-stations of warbler presence exceeds total number of point-counts because both species were recorded at some sites.

Month	# of point-counts	Major landscape form					
		Plains	Coast	Wetlands	Highlands	Developed	Inshore
June	46 (15) [17]	12 (8) [3]	8 (3) [2]	8 (2) [3]	6 (0) [4]	7 (2) [2]	5 (0) [3]
September	50 (6) [27]	19 (2) [10]	5 (0) [1]	3 (0) [3]	14 (1) [9]	9 (3) [4]	0 (0)[0]
February	67 (23) [18]	29 (12) [6]	1 (0) [0]	14 (4) [9]	17 (6) [1]	0 (0) [0]	6 (1) [2]
May	61 (20) [33]	16 (9) [5]	2 (0) [1]	13 (3) [12]	12 (4) [2]	12 (3) [9]	6 (1) [4]

Table 3.6: Correlation matrix of all measured variables shows no significant correlation between pairs.

	YWp	**BWp**	**L Scape**	**C Cover**	**Veg**	**Anthro Dev**	**VegStr**	**C Height**	**Dom PlSp**	**Fol Den**	**Topo**
YWp	1.00	0.07	0.15	0.04	-0.04	0.11	0.06	0.10	0.14	0.03	-0.08
	BWp	1.00	-0.03	-0.02	-0.19	0.01	0.00	-0.14	-0.02	0.00	0.09
		L Scape	1.00	0.05	0.09	-0.24	-0.01	0.13	0.16	0.19	-0.23
			C Cover	1.00	0-.18	-0.18	-0.28	0.34	0.09	0.32	0.02
				Veg	1.00	-0.14	0.07	0.08	0.00	0.12	-0.18
					Anthro Dev	1.00	0.02	-0.11	0.15	-0.26	-0.11
						Veg Str	1.00	-0.31	-0.12	0.07	-0.01
							C Height	1.00	0.12	0.21	-0.06
								Dom PlSp	1.00	-0.03	-0.15
									Fol Den	1.00	-0.05
										Topo	1.00

Table 3.7: Analysis of variance table: Barbuda Warbler (output from R).

Model	Residual Degrees of Freedom	Residual Deviance	Degrees of Freedom	Deviance	AIC	Pr (>Chi)
Null	224	266.17			268.2	
Full	149	171.28	74	94.89	321.28	0.05139

Table 3.8: Analysis of variance table: Yellow Warbler (output from R).

Model	Residual Degrees of Freedom	Residual Deviance	Degrees of Freedom	Deviance	AIC	Pr (>Chi)
Null	223	304.74			306.7	
Full	149	181.36	74	123.36	331.36	0.0002806

Table 3.9 a & b: BWPresence (BWp) and YWPresence (Ywp) are reduced to suites of models which are better at explaining the presence of both warbler species better than the null models. The explanatory variables presented in each reduced model are more influential to the presence of Warblers than the removed variables. Delta AIC values (differences between AIC of the ith model and model with lowest AIC) are presented as a measure of model strength. Each global model underwent 10 iterations of subtractive reduction.

a) Barbuda Warbler Presence

Rank (by Delta AIC)	**Variables**	**Log-likelihood**	**AIC**	**Delta AIC**	**Akaike weight**	**Evidence Ratio**
1	Canopy Height	-130.58	267.16	0	0.49	1
2	Yellow Warbler presence; Canopy Height; Temperature	-129.73	269.47	2.31	0.15	3.17
3	Yellow Warbler presence; Canopy Height; Temperature; Anthropogenic Development	-129.69	271.39	4.23	0.06	8.30
(Global Model) Barbuda Warbler Presence	Yellow Warbler presence; Landscape form; Canopy cover; Vegetation; Anthropogenic Development; Vegetative strata; Canopy Height; Dominant plant species; Foliage density; Temperature	-87.31	314.62	47.46	$2x10^{-11}$	$2x10^{10}$

b) Yellow Warbler Presence

Rank (by Delta AIC)	**Variables**	**Log-likelihood**	**AIC**	**Delta AIC**	**Akaike weight**	**Evidence Ratios**
1	Landscape form	-141.17	294.33	0	0.45	1
2	Landscape form; Vegetation	-132.69	295.37	1.04	0.27	1.68
3	Landscape form; Vegetation; Temperature	-132.25	296.50	2.17	0.15	2.96
4	Landscape form; Vegetation; Temperature; Canopy Height	-131.14	298.28	3.95	0.06	7.21
5	Landscape form; Vegetation; Temperature; Canopy Height; Vegetative strata	-124.53	299.05	4.72	0.04	10.59
(Global Model) Yellow Warbler Presence	Barbuda Warbler presence; Landscape form; Canopy cover; Vegetation; Anthropogenic Development; Vegetative strata; Canopy Height; Dominant plant species; Foliage density; Temperature	-98.66	337.31	42.98	$2x10^{-10}$	$2x10^{9}$

CHAPTER 4

INVESTIGATING SEASONAL PATTERNS OF BREEDING AND MOULT IN BARBUDA AND YELLOW WARBLERS

Seasonality may influence habitat and distribution patterns described in Chapter 3. Reasonably, birds' activities across their annual cycle are related to the location and nature of selected resources. However, seasonality is useful to know in its own right, particularly in the case of the Barbuda Warbler, as this aspect of the species' biology was never investigated.

Procedure

Catching the birds was necessary to colour-band them, and to acquire data on body condition and feather moult. Measured-effort mist-netting (Ralph *et al*. 1993; Pyle 1997) at 29 stations (Figure 4.1) was used to colour band birds and document reproductive condition. One 6-m mist-net (24-mm mesh size; 4-shelf) was used at most times during netting sessions, sometimes a combination of two 6-m nets angled through gaps in the vegetation. Nets were open between 06:00 and 11:00. Audio equipment (3rd Generation iPod Nano connected to a 2 x 5-cm speaker set-up) functioned as a lure and was set up close to the net at a height of ~1 m, whereby both warblers' songs were played back alternately throughout each mist-netting session. Upon capture, each bird was fitted with a unique combination of three coloured, plastic leg bands on the left leg, and one aluminium (United States Geological Survey [USGS]) Bird Banding Laboratory (BBL) leg band on the right. This banding later identifies the individuals in the field, facilitating collecting observations of known individuals. Netted birds were examined for the

presence of a brood patch (females) or a cloacal protuberance (males). Only females develop a brood patch in Yellow Warblers (Lowther *et al*. 1999); and only females incubate in the closely related (to the Barbuda Warbler) *S. adelaidae* (Toms 2010a). Exposed culmen length, natural wing chord, and mass of each warbler were recorded; a few feathers were plucked from each warbler's breast for later genetic sexing**.** Mist netting was repeated at arbitrarily selected sites (Figure 4.1), and at sites where unbanded birds showed breeding behaviour such as territoriality, feeding/begging, or singing.

Photographs of the birds in hand were taken to check and provide a permanent record of plumage and reproductive characteristics, and also assist in aging and sexing (Pyle 1997; Toms 2010a). Feathers were scored from missing or new in pin to new feather fully grown (De Beer at al. 2001). Moult of body (contour) feathers was also recorded separately, though more emphasis was placed on analysis of wing and tail moult. Measurements of natural wing chord and mass made in the field were used to explore any trend in size-corrected mass across field trips (Figures 4.5 & 4.6). Presence of an incubation patch (vascularised, oedematous bare skin on belly) or, in males, a swollen cloacal protuberance, were noted as signs of active breeding.

Field recordings of obvious behavioural cues of breeding such as display and copulation were recorded, and sites of such behaviour were marked and monitored for additional breeding observations. Individuals carrying nesting material were followed as discreetly and for as far as possible, or until we were led to a nest. If found, the nest was monitored until the outcome of the nest was deemed successful or unsuccessful (Wiewel 2011). The nest was marked, photographed, and measured when the bird left on its own volition. Fledglings accompanying adults indicate recent successful breeding (Diamond

1974; Gunn *et al*. 2000); if suspected, such a pair was followed while making attempts to capture photographs or video.

In many tropical areas, increased sustained rainfall coincides with the breeding season of passerines (Staicer 1991, 1996b; Nakamura 1995; Toms 2010a, b; but see also Diamond 1974). Normally, the onset of the wet season coincides with flowering and fruiting of plants, which in turn partly determines the diversity of the warblers' prey. Rainfall data obtained from Antigua & Barbuda Meteorological Services are illustrated along with various observations of reproductive behaviour in both warbler species; and systematic observations of plants in flower or fruiting made between point counts. If I saw a flower, a fruit, or a seed on the plant before, during, or after I counted birds at a sample station, or later in a photograph of plants there, I wrote down those plant species as "in flower," or "fruiting". Photographs of the vegetation at the sample-station were taken after point-counting to later identify the dominant plant species, according to Pratt *et al*. (2009). Photographs of fruits or flowers on the plants at the sample station helped to identify the species, as well as provided a record of seasonality of such species, important for the general ecological knowledge within this investigation.

Numbers of both species detected were unequally distributed across sample months. Standard deviations of counts among months are also variable and for these reasons, the non-parametric Kruskall-Wallis test was used to determine if there are statistically significant differences in the number of detections among sampling months. The null hypothesis tested here is that there is no difference in warbler detections among survey months.

Results

Mist netting: 30 Barbuda Warblers and 35 Yellow Warblers were caught and banded from ~90 hours of mist-netting sessions during this survey's four field-trips. Though mist-netting was repeated at a few sites, sometimes at the exact same spot, no birds were re-captured from previous netting sessions. Only two resights were made: a Barbuda Warbler was seen foraging ~ 200 m from where it was banded; and a Yellow Warbler foraging ~ 800 m from where it was banded. Tables 4.1 and 4.2 summarise the capture data (age and sex) for all four trips.

From these mist-netting data alone (i.e. not considering field observations and information from re-sights), one Barbuda Warbler (one of four adult females) and one Yellow Warbler (one of eleven adult females) were confirmed breeders. Of these two, a vascularised brood patch was observed on the Barbuda Warbler (After Second Year, ASY; June 5, 2013); and a smooth brood patch on the Yellow Warbler (ASY; May 20, 2014). The presence of cloacal protrusions in males (4 of 21 Barbuda Warblers; 6 of 22 Yellow Warblers) indicated that those individuals were probably breeding, though it was uncertain if they were recently paired or were already brooding chicks. Four Barbuda Warbler males and seven Yellow Warblers (six males, one female) were probably breeding, based on the presence of prominent cloacal protrusions and 23 Barbuda Warblers and 25 Yellow Warblers were deemed possible breeders based on age (after hatch year birds) and small cloacal protrusions (Table 4.2). No birds in their first calendar year of life were caught.

Field observations: No other clues (such as fat scores) were strong enough from mist-netting data to verify timing of breeding by either warbler species. But some

behavioural observations from the field can perhaps increase the confidence in estimating the timing of breeding. A summary of breeding season cues from approximately 350 hours of field observations and re-sights is presented graphically for both warbler species (Figure 4.3). Reproductive behaviours during courtship were most numerous in May and June, and include singing from specific perches and intra- and inter-specific chases within and around the areas of those perches. Confirmed copulation, and nesting, were observed separately for Yellow Warbler in May. Flowering and fruiting plants (including exotic species in domestic gardens) were recorded during and between point-counts (see Chapter 4, Procedure), and illustrated alongside occurrences of reproductive behaviour. Detections were easier when singing occurred conspicuously, such as continuously from a single perch or from a specific array of perches (thus indicating a possible territory).

Rainfall and plant phenology: Figure 4.4 shows an unusual peak in December 2013, and that there was lower rainfall from September-November 2013 than the historical average. The chart illustrates only recent recordings during and between sampling months; however in May 2013 Antigua and Barbuda Meteorological Office recorded four times the historical (May's) rainfall. Following such extreme rainfall (June 2013) were peaks of vegetative flowering and fruiting, and warbler reproductive behaviour (Figures 4.2-4.4). On the following field-trip, in September 2013, there were relatively few detections of warblers during point-counts and mist-netting, but clear signs of moult in the general bird-community. Additionally, there were relatively few observations of plant flowering and fruiting, and none of warbler reproductive behaviour.

Moult: Although few warblers were caught, evidence of moult in each species is still available (Table 4.2); however the absence of this evidence from only a sample of

the population (such as in February) does not necessarily mean that no birds were moulting. Of the photo-set (wing-spread, mantle, tail-spread, and face) only one wing was recorded, but data reflect results from field observations of both wings, as well as of the contour and body feathers. Only one instance of adventitious moult (asymmetrical moult, indicating possible accidental feather loss) was observed and is not included in calculations or illustrations. One Barbuda Warbler caught in May (SY Male) had no tail, possibly because of stress moult. Only three individuals were caught in September, when the generally secretive behaviour of both species, and the moult evident in other species seen and caught, would suggest that warblers were moulting then.

Body condition: Since no sub-cutaneous fat in captured warblers was observed, an indication of condition (breeding preparedness) from fat scores is not directly available. Size-corrected mass (mass divided by winglength) is an alternative way to assess seasonal changes in body condition (Figures 4.5 & 4.6). Plots of birds' body condition in September are included as single data points as only three individuals were caught. The spread of data indicates that Barbuda Warblers captured in June 2013 and May 2014 were similar in body condition relative to the other field trips, based on positions of the medians and lower quartile groups and likewise for captured Yellow Warblers in February and May.

Barbuda Warblers showed significant differences in indices of body condition among months: ANOVA $\mathbf{F}_{calc.}$ (3, 24) = 6.590; p = 0.002. A post-hoc Tukey test showed that indices of body condition were significantly higher in June than in February: $\mathbf{Q}_{calc.}$ = 5.85; p = 0.002. Yellow Warblers showed no significant differences in indices of body

condition among June, February and May (omitting September because there was only one point): ANOVA $\mathbf{F}_{calc.}$ (2, 30) = 0.79; p = 0.463.

Combining results from June 2013 and May 2014 (reproductively active months), and the results from September 2013 and February 2014, the ANOVA was repeated to test for significant differences in either warbler's size-corrected mass between the June/May and September/February combinations. Barbuda Warblers showed significantly higher indices of body condition between June+May than in September+February: ANOVA $\mathbf{F}_{calc.}$ (1, 26) = 5.170; p = 0.031. Yellow Warblers showed no significant differences in indices of body condition between June+May and September+February: ANOVA $\mathbf{F}_{calc.}$ (1, 32) = 1.782; p = 0.191.

In addition to the indices of body condition, comparisons of physical dimensions can be made given these data (Table : captured Yellow Warblers were 1.5 times heavier than Barbuda Warblers (Student's t-test statistic = 15.17; d.f. = 60; $p < 0.0001$), have 1.2 times longer natural wing-chord (t = 22.37; d.f. = 60; $p < 0.0001$), but have only 1.05 times a longer bill (t= 2.28; d.f. = 52; p = 0.03).

<u>Point count data:</u> Point count data revealed that Barbuda Warblers were least detected in September, the month when Yellow Warblers were second most detected (among months). Analysis of point-count Barbuda Warbler abundance data, showed a statistically significant monthly difference in the distributions of Barbuda Warbler abundance across sample points (Kruskal-Wallis test $H_{adjusted}$ = 8.539; d.f. = 3; p = 0.036). Post-hoc Dunn's Test showed that abundances were significantly higher in June (***p*** = 0.026), February (***p*** = 0.010), and May (***p*** = 0.015), when compared with September's counts. Yellow Warblers similarly showed unequal abundance by month (Kruskal-Wallis

test $H_{adjusted}$ = 14.262; d.f. = 3; p = 0.003). Post-hoc Dunn's Test showed that abundances were significantly higher in May than in February (***p*** = 0.001); and significantly higher in February than in September (***p*** = 0.003). The post-hoc calculation did not reveal any other significant differences in Yellow Warbler abundances among months. From a density-per-sample-station perspective, both warblers were least detected in February, and most in June. In September and May, Yellow Warbler detections were five to six times as numerous as Barbuda Warbler detections.

Seasonality of habitat selection: There is an apparent pattern in both warblers' distribution across broad landscape forms. In May, there were more Barbuda Warblers detected per point in the Plains than in any other landscape form; in May the Yellow Warbler was relatively less abundant than the Barbuda Warbler in the Plains, but was considerably more abundant than the Barbuda Warbler in Mangrove. The Yellow Warbler was generally more abundant than the Barbuda Warbler across all months, but the difference was most pronounced in May.

Discussion

Breeding & moult: With data from only parts of two annual cycles (2013 and 2014) little can be concluded about the normal seasonality of these species at this site, particularly in view of the anomalous rainfall patterns in the study years. However the patterns suggested do coincide generally with expected seasonality of songbirds in the northern Caribbean (Diamond 1974), with breeding concentrated in May/June and a moult in autumn.

Barbuda and Yellow Warblers both exhibited reproductive behaviour in June 2013 and May 2014. If setting up of territories defines the beginning of the breeding season, a preliminary conclusion (from Figure 4.3 and from between-sample-session field observations) is that both species began breeding in May. This breeding pattern seems similar to passerines of more northern climates, and overlaps with more southern species which have several breeding attempts throughout the year. Based on the northern patterns, perhaps there is a similar peak in food species on Barbuda, brought about by the rainfall-influenced plant-flowering patterns. A closer look at the plant phenology in association with the arthropod food species of these warblers would be necessary to investigate whether food abundance explains bird seasonality. An absence of warblers from food-scarce areas during May and June may be expected. Figure 4.3 also illustrates adult pair observations of the Yellow Warbler in three of the survey months. This probably indicates a long-term pair bond in this species, but has yet to be verified.

Overlap in breeding and moulting of both warbler species in May and June (Figure 4.3, Table 4.2) may be interpreted as captured individuals beginning moult and some completing. The reproductively active periods of both species may be longer than

detected. Moult would be expected to continue into September but since only three warblers were captured then, likely because of reduced flight activity during moult, definitive conclusions cannot be made.

Mist netting: Higher numbers of captures appear to coincide with the survey months of increased reproductive behaviour (Table 4.2, Figure 4.3). This suggests that reproductive behaviours such as courtship display, singing and chases increase the detectability of the birds; and perhaps these behaviours render them more net-prone: quite likely, as observations of Yellow Warbler territoriality suggest. Nets were set up near what appeared to be warbler breeding territory or home range. Birds move around locally there, and often the same bird was caught several times during the same mist-netting session. From the data collected, it is not known if birds defend territories year-round.

Field observations: Bird activity from field observations and mist-netting suggest that birds were most active when breeding, and least when probably moulting. Data from this study are not sufficiently robust to definitively identify the main moulting season of these warblers.

Rainfall and plant phenology: Mist netting (Table 4.2, and Figures 4.5 & 4.6) and field observations (Figures 4.2A & B; Figure 4.3) show results that suggest seasonal variation. Signs of reproductive activity begin in May, and show a peak in June. These coincide with the flowering and fruiting peaks of the vegetation at sample stations, which in turn coincide with relatively lower rainfall on Barbuda during these survey months. McSweeny *et al.* (2012) identify May-October as Barbuda's rainy season; Antigua and Barbuda Meteorological Services identifies October as the peak rainfall month (1993-2014); and December was identified during this survey-year (2013-2014) as the peak

rainfall month. Though plant phenology is quite varied (and its investigation beyond the scope of this work), it is a reasonable premise that flowering peaks just before the rainy season (Bawa *et al*. 2003), so fruit ripening and subsequent seed dispersal and germination occur at the onset of the rains. If the plants on Barbuda respond to their environment in the same season of the stimuli, then the peaks of reproductive behaviour observed in June 2013 (as well as moulting in this month) and May 2014 may be interpreted as timed to plant phenology. The monthly distribution of rainfall during this study was anomalous with respect to the long-term average, so observed seasonal patterns may not be typical. Interpreting the ecological response to this exceptionally heavy rainfall (in May 2013) may be useful for discussing warbler presence and behaviour in the following month of June (survey's first trip); there can probably be significant short-term impacts on phenology (Corlette and Lafrankie 1998), and resultant changes in the spatial and temporal distribution of selected resources (Shaik van *et al*. 1993), and associated warbler presences.

Body condition: Fat was absent from all but one Barbuda Warbler in June, deemed to be brooding young. The absence of fat is most likely attributed to the fact that the birds captured were residents; migrants are long-distance travellers and have more need for extensive fat stores (but see Diamond 1974).

The index of body condition is presented to compare the physical condition of the warblers examined. Warblers with a higher index are considered in better physical condition relative to warblers with a lower index. Thus Barbuda Warblers appeared to be in "better" condition during reproductively active months (May and June) than in February and September. I believe the demand on the ability of the bird to provide for

itself within its niche is relatively greater during the reproductively active periods, as the biological processes are energetically expensive for the bird. The bird's energy reserves, therefore, will be boosted by fattening (or perhaps increased protein reserves (Angelier *et al*. 2011)) to accommodate for this expense.

Though this study does not aim to investigate drivers of change in body condition, it is important to note that body condition is not exclusively associated with breeding preparedness. The highest and lowest indices of both warblers' body condition occurred in June and February respectively. Along with increasing resources for breeding activities (such as egg-laying laying or increased food intake), embedded in these indices are also the effect of rainfall and water availability on the phenology of plants selected for warbler use (Figures 4.2 C & 4.4). Changes in phenology of warbler-selected plants (as resources) will indirectly affect the body condition of those warblers by affecting the productivity, abundance and distribution of their arthropod prey that use those plants (Angelier *et al*. 2011). Food availability data would be optimal for further investigations of changes in warbler body condition.

Chapter 5 presents a general discussion which attempts to synthesise the points made in the previous chapters. The aim is to facilitate a broad perspective of why the focal warbler species are where they are.

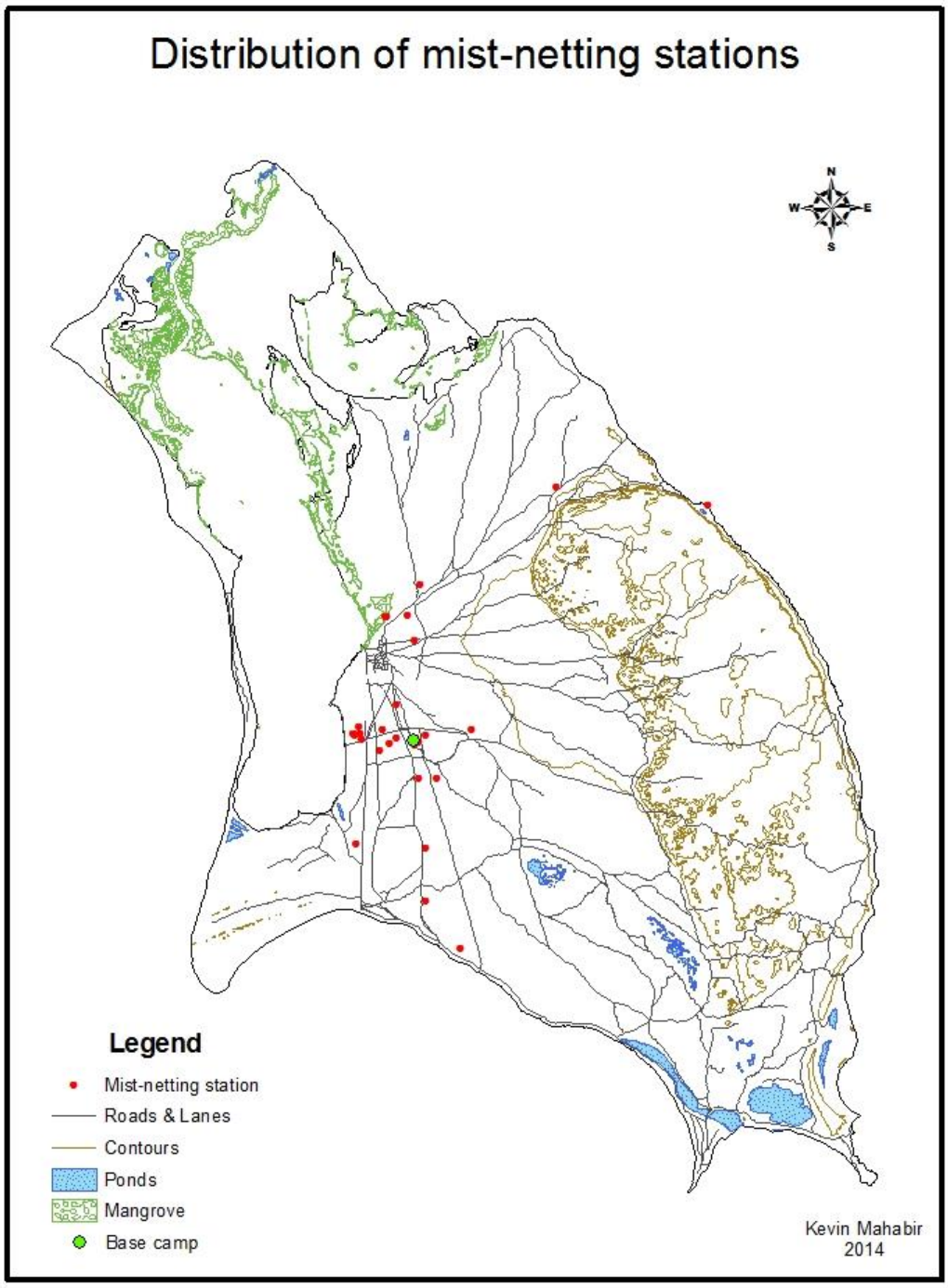

Figure 4.1: Distribution of mist-netting stations was opportunistic and mainly targeted terrain such as developed areas and lowland scrub close to base camp.

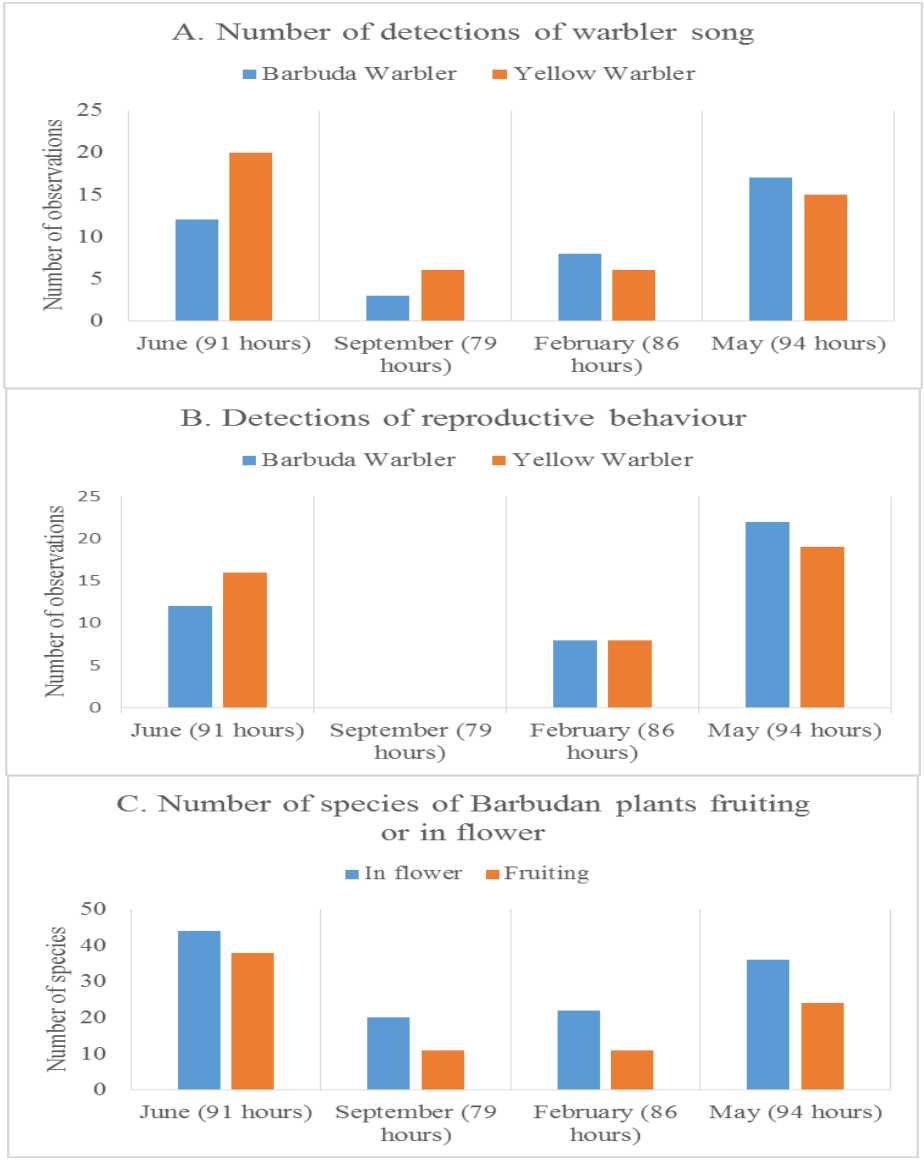

Figure 4.2: Floristic phenology and warbler reproductive behaviour recorded during and between point-count sampling, June 2013 - May 2014. # of hours of effort per trip varied with weather and our physical condition. (**A)** Singing was recorded during all survey trips, albeit considerably decreased in September **(B)** Summing detections of reproductive behaviour per trip shows peaks in June and May; and zero in September partly due to the relative inconspicuousness of birds then. **(C)** Numbers of species of plants in flower and fruiting were highest in June and May, corresponding to peaks in detections of reproductive behaviour.

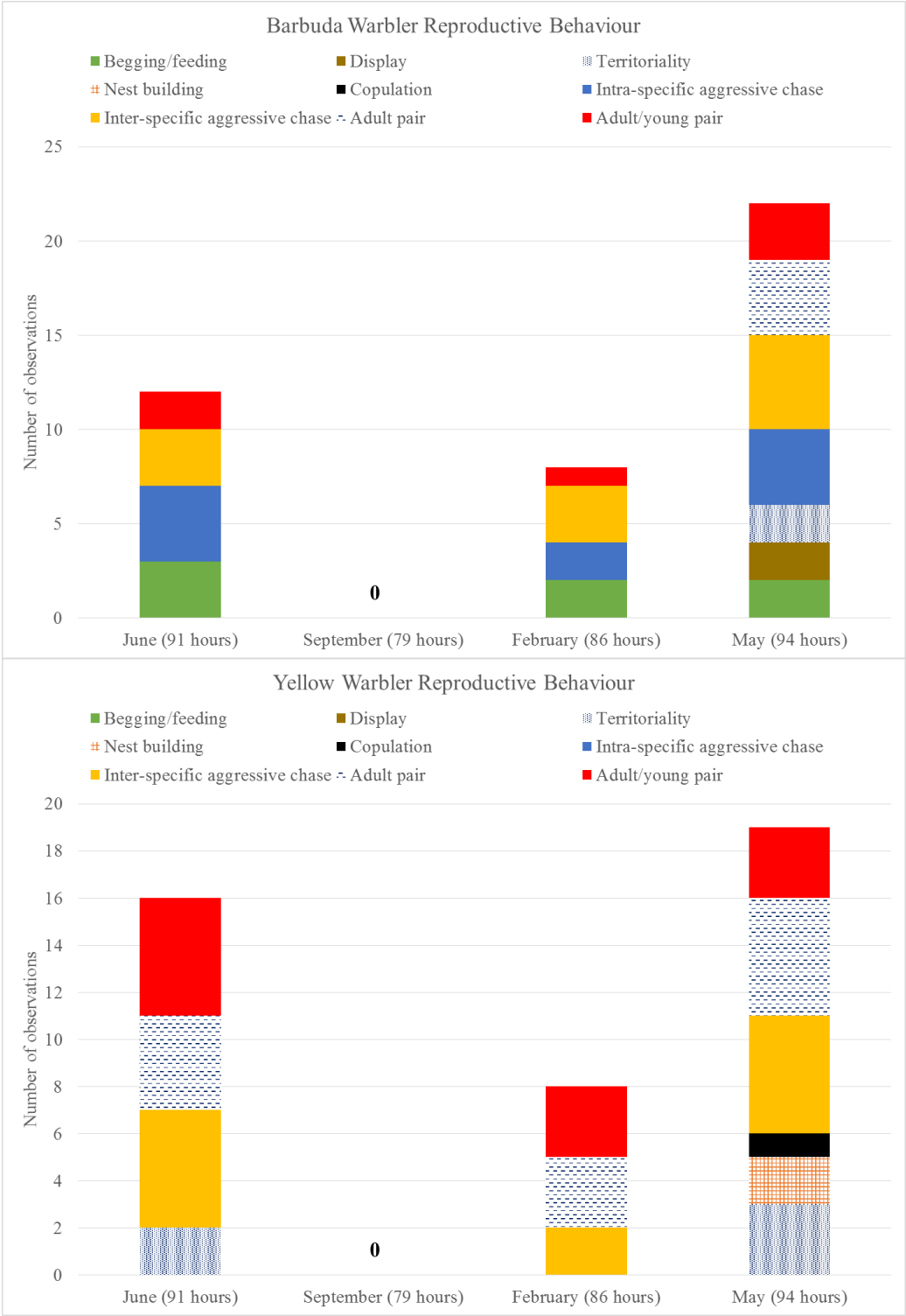

Figure 4.3: Recordings of specific reproductive behaviour from ~350 hours of field observations. Like warblers' singing, reproductive behaviour was at its lowest in September, corresponding to the reduced flowering and fruiting of plants.

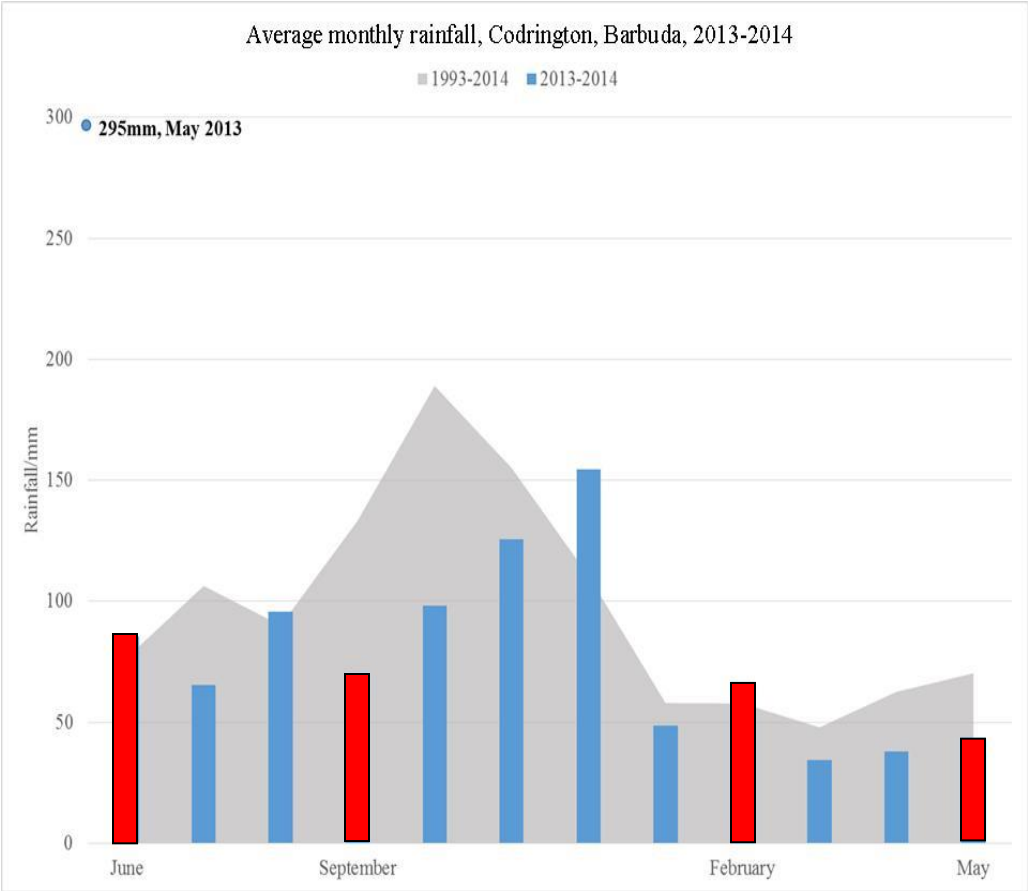

Figure 4.4: Average rainfall, Codrington, Barbuda, 2013-2014 (Antigua & Barbuda Meteorological Services) was similar to historical average in June and February, but lower in September and May. 295 mm of rainfall was recorded in May 2013 – four times the average historical amount.

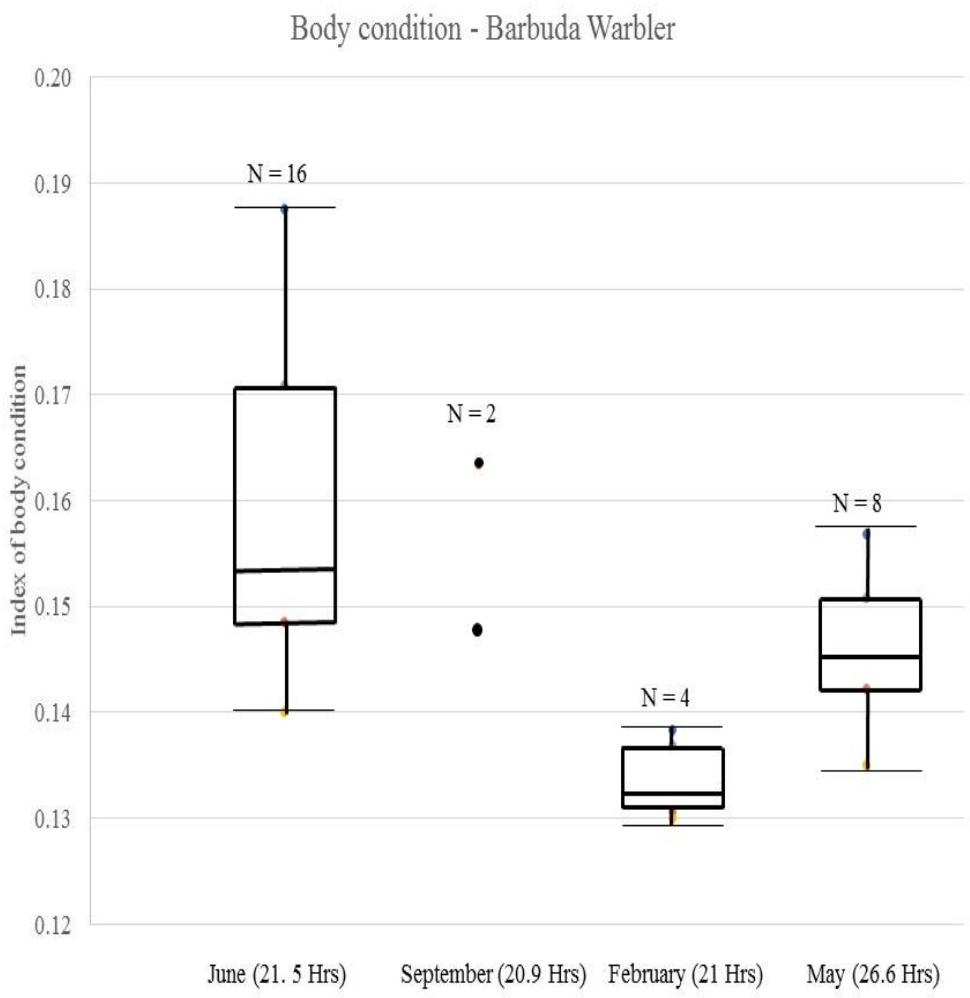

Figure 4.5: Ilustration of body condition (or size-corrected mass: mass/natural wing chord) of Barbuda Warblers per field trip, June 2013 – May 2014.

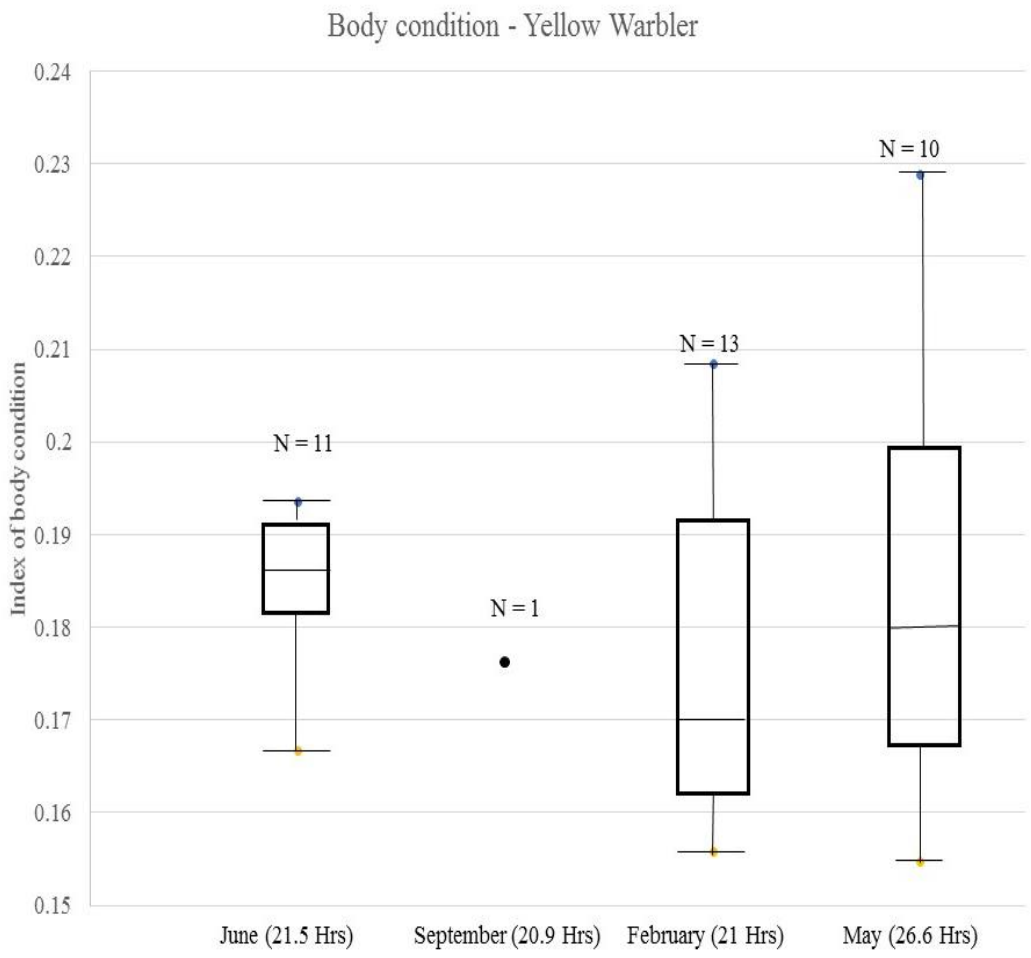

Figure 4.6: Illustration of body condition (or size-corrected mass: mass/natural wing chord) of Yellow Warblers per field trip, June 2013 – May 2014.

Table 4.1: Summary of mist-netting data for all field trips.

M – Male; **F** – Female; **HY** – Hatch Year; **SY** – Second Year; **ASY** – After Second Year; **AHY** – After Hatch Year; **Undet -** Undetermined

		Age				
	Sex	**HY**	**SY**	**ASY**	**AHY**	**Undet**
Barbuda Warbler	***M***	0	8	9	4	0
	F	0	1	3	0	0
	Undet	1	0	0	3	1
Yellow Warbler	***M***	0	5	16	1	0
	F	0	2	8	1	0
	Undet	0	0	0	0	2

Table 4.2: Presence of moult from mist-netting data (30 Barbuda Warblers (BW) and 35 Yellow Warblers (YW) captured in total, from ~ 90 hours of mist-netting) is recorded as the number of individuals replacing contour (body) feathers, or feathers of the wing (primaries, secondaries, and their coverts) or tail (rectrices)

	June			September			February			May		
	Body	Wing/tail	N	Body	Wing/tail	N	Body	Wing/tail	N	Body	Wing/tail	N
BW	4	1	15	0	0	2	0	0	4	0	0	9
YW	2	0	10	1	0	1	0	0	13	0	1	10

Table 4.3: Comparison of weights and measurements (and standard deviations) of captured Barbuda and Yellow Warblers

	Yellow Warbler	Barbuda Warbler	Ratio Yellow Warbler/Barbuda Warbler
Mass/g	10.79 ± 0.93	7.60 ± 0.77	1.42
Wing chord, mm	59.52 ± 3.03	49.63 ± 1.42	1.20
Bill length, mm	10.73 ± 0.93	10.23 ± 0.58	1.05

CHAPTER 5

GENERAL DISCUSSION

My research proposed specifically to:

1. Document and compare the current distribution of Barbuda and Yellow Warblers on Barbuda;
2. Identify attributes of the environment used by Barbuda and Yellow Warblers across their annual cycles on the island; and
3. Describe the local annual cycle of the Barbuda Warbler.

In addition to pursuing these specific objectives, this study provides somewhat of a foundation to explore the broader ecological interest in resource partitioning between two congeneric species of insectivorous bird in the depauperate environment of a low-lying tropical island.

Because I was unable to replicate my work across multiple seasons, I cannot draw strong conclusions about potential trends and inter-annual variation in distribution, habitat associations, and reproductive behaviour. Nevertheless, I attempt to synthesise the findings thus far.

My emphasis was on establishing basic ecological facts of the distribution and ecology of a poorly-known endemic species, but its relationships with a much more widespread and better-known congener may be of more general significance because of the relative rarity of co-existence of two such similar species on a small remote tropical island. The relationships between these two focal species allow examination of concepts of co-existence and competitive exclusion.

The observation that both Barbuda and Yellow Warblers apparently began breeding in May is coincident with northern hemisphere passerines' breeding patterns in general; even at Barbuda's tropical latitude, warblers breed here at the same time of year as further north and elsewhere in the Caribbean (Diamond 1974). Tropical birds' breeding seasons are commonly influenced also by rainfall, which in this study peaked in May (but was exceptional compared with the usual pattern), precluding the possibility of separating rainfall from seasonality as a cue for breeding. Elsewhere in the northern Caribbean passerines also exhibit this pattern, for example in the resident Yellow Warbler subspecies complex at similar latitudes (Salgado-Ortiz *et al*. 2008; Lowther *et al*. 1999; Diamond 1974), and the closely-related Adelaide's Warbler *Setophaga adelaidae* in Puerto Rico (Toms 2010a).

The point counts throughout the island reveal low co-occurrence between warbler species. There is probably a limited resource common to both warbler species which influences their occurrence. Depending on the spatial scale of consideration, co-occurrence at a vegetation stand level may be apparent, but within such a distribution, there may be finer-scale segregation between warbler species (such as what was found). Such a distribution may be viewed as a way of avoiding competition for the assumed limited resource. Yellow Warblers demonstrate this with prominent presence in the mangroves, perhaps being outcompeted by the Barbuda Warbler at a fine resource level in the Plains, and selecting from the persistence of arthropod prey in Mangrove growth. Mangroves are in the wettest areas of the island, presumably supporting relatively abundant warbler arthropod prey during periods of low rainfall. If the wet mangrove

habitats improve arthropod productivity, then resource selection within this habitat may reduce food stress in the driest months (Angelier *et al*. 2011).

From banding measurements, mean mass of Yellow Warblers was greater than that of Barbuda Warblers. It is possible in this case that the size of a species influences its habitat use. Table A, Appendix, provides measurements of Barbuda and Yellow Warblers which may support preliminary analyses of patterns. Compared to Barbuda Warblers, the heavier, larger, longer-winged Yellow Warblers may have an advantage in competitive interactions. Perhaps the larger species may exclude the smaller; or a difference in foraging ecology may be developed to "mediate between demographics and habitat quality" (Latta and Faaborg 2001; Luther and Greenberg 2011).

In this study, ecological segregation based on food selection may not be the cause of the spatial avoidance found between Barbuda and Yellow Warblers. Schoener (1965) proposes, at least for sympatric species, niche partitioning with the aim of reducing competition may be driven by microhabitat selection according to micro-ecological separation of small-sized food. Schoener's (1965) study related that the foraging implications of large bill length ratios (of sympatric congeners) may be the drivers of ecological segregation among the study species. But because of the small (5%), albeit significant (p = 0.03) difference in bill lengths between Barbuda and Yellow Warblers, the selected food sizes will have an associated relatively narrow range. So the spatial avoidance between warbler species suggested in this study may be viewed as an alternative method of ecological segregation brought about by the measured 95% similarity in bill length, which may not have allowed for much segregation by food.

Canopy height, a variable significantly associated with Barbuda Warbler presence, shows little variation across the points sampled. The highest category, 20-30 m, is available only in the coconut plantation to the south-west of the island and no warblers were detected there. Map and photograph analysis show that high canopied trees are emergent in the Plains and Highlands, where the Barbuda Warbler seems to replace (or exclude) the Yellow Warbler.

Though the models predict that, to a lesser degree, Yellow Warblers are also supported by high-canopied trees, it seems that either the Mangrove growth on the island provides such a canopy, or maybe there is a resource still to be measured on a finer scale within the Mangrove. But based on Latta and Faaborg (2001), further investigation on foraging ecology as a driver of ecological segregation will present valuable ecological data on the scarcely-studied Barbuda.

Though detecting competition cues requires many more hours of behavioural observations, and there is only circumstantial evidence of competition (aggressive interspecific chases), perhaps behaviour consistent with interspecific interactions (along with possible limited resources common to both species) between Barbuda and Yellow Warblers accounts for their mutual avoidance, thus reducing competition. While Diamond (1973) observed spatial segregation between these two species on another island, suggesting that such a distribution may arise from territorial avoidance, this study specifies that they are also somewhat separated ecologically, according to resource selection. Though rare for species as ecologically similar as these, their co-existence observed in this study can be expected, considering Diamond's (1973) observations. If both warblers are indeed competing for resources, space included, there is a fine-scale

ecological separation which merits further investigation. The dynamics of their apparent co-existence (in the same localities) serves to minimise potential competition. Their mutual niche partitioning process in a highly homogenous environment such as Barbuda may be observed by studying their food, as their prey species may be involved in micro-niche partitioning of their own (Schoener 1965 Luther and Greenberg 2011), "luring" the respective warblers into micro-habitat "zones" that are not tangible to human observation. The warblers' foraging strategy, morphological or sexual advantages, or their foraging strata/zones may reveal information about their respective resource selection hierarchical processes and life-histories that were developed to co-exist with minimal competition. Studies spanning more than one annual cycle of the focal warblers' lives may improve this study's interpretations of seasonal distribution. Shifts in precipitation influence the availability of resources throughout the annual cycles, so changes in warbler inter- and intra-specific interactions and distribution across wet and dry seasons may be evident. Observations in future studies should be made to better interpret interspecific interactions as cues for competition. Pianka (1974) provides a guide, suggesting that increased demand for a similar resource that is in abundance may result in observations of local co-existence, as the potential competitors may equilibrate with interspecific tolerance (of each other as well as of resource use).

In addition to niche overlap, there is also the consideration of one warbler's niche completely enclosed within the niche of the other. Intensive studies on interspecific interactions may reveal more about this potential scenario, which may develop from differential competitive abilities, resulting in the competitively superior warbler occupying a niche included within the niche of the other. Future monitoring may even

reveal another possibility, where niches do not overlap, in the interest of competition avoidance. Perhaps this may be observed as the absence of direct interspecific interactions, but this may be unlikely given the conditions at the time of this study. Now, after the environmental disruption of hurricane Irma, the relationship between competition and ecological overlap of the focal species in a destabilised environment will be relatively difficult to quantify; but the intention to investigate must carefully include implications of the recent disaster, e.g. selected-resource economics (of supply and demand), and the resultant fragmentation of resources and warbler populations.

The Barbuda Warbler's endemic status contributes to its inherent vulnerability in case of a local natural disaster e.g., a hurricane such as what swept through the island in 2017. Before anthropogenic land development was intensified (post-slavery), there may have been a different suite of resources, or more extensive resources, from which to select. It is likely that the interspecific interactions reported by Diamond (1973) and Einarsson (2007) may not have resulted in exclusion if the resources were less fragmented and more abundant. Future monitoring should facilitate documenting species occurrence along with habitat measurements, as well as demographic studies. Identifying changes in the species' body condition (e.g., spatial trends in size-corrected mass) along with environmental stresses will help researchers focus on the period of the annual cycle that is most important for the bird's survival.

In conclusion, the single-island endemic Barbuda Warbler was found to co-exist on the island with the Yellow Warbler, a larger and more widespread potential competitor with a similar annual cycle. From examination of ecological models, they both used subtly different components (resources) of the available environment (habitat), in which

the presence of high-canopied trees appears to be closely associated with the presence of Barbuda Warblers. Wetlands and mangrove growth appear to be closely associated with the presence of Yellow Warblers. Furthermore, analyses of this study's data presented a finer perspective of ecological segregation, whereby interspecific interactions are shown to be significantly informative to the ecological niche occupancy of these species. Because of the small differences in bill sizes between them, they may capture similar food, and thus choose to reduce competition (and hence enhance co-existence) by means (such as foraging strategy) driven/supported by differences in body condition or morphological variations (such as physical size or wing length).

The result that the Barbuda Warbler avoids the Yellow Warbler, but not the reverse, updates what is known of the ecology of the Barbuda Warbler. In particular, the case of Barbuda Warblers' interactions with Yellow Warblers may now be better addressed given these data.

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APPENDIX I: Table A – Table of Barbuda and Yellow measurements by month. Bill length was included in measurements after work at two mist netting stations. Birds which escaped before measurements were taken were omitted from this table and analyses.

Month	Species	ID	Sex	Age	Wing chord/mm	Mass/g	Mass/Wing chord	Bill length/mm
June	BWAR	BRB	M	AHY	50	7	0.14	
June	BWAR	BRW	U	AHY	51	7.5	0.15	
June	BWAR	BYB	M	AHY	50	7.5	0.15	
June	BWAR	WBW	F	ASY	49	7.5	0.15	
June	BWAR	BGB	U	HY	49	8	0.16	
June	YWAR	BWB	M	ASY	63	11.5	0.18	
June	YWAR	BGW	M	ASY	62	11.5	0.19	
June	BWAR	WRG	M	SY	47	7	0.15	9.8
June	YWAR	YWR	M	ASY	63	10.5	0.17	10
June	BWAR	BGY	M	ASY	51	7.5	0.15	10.1
June	YWAR	RWG	M	ASY	61	11.1	0.18	10.2
June	BWAR	BRY	U	AHY	48	9	0.19	10.2
June	BWAR	BWY	M	ASY	52	8	0.15	10.3
June	BWAR	RGY	M	ASY	49	7.5	0.15	10.4
June	BWAR	BRG	M	SY	49	8.5	0.17	10.4
June	YWAR	BYG	F	ASY	59	11	0.19	10.7
June	BWAR	BYR	M	SY	50	8	0.16	11
June	BWAR	YBY	M	ASY	50	8.5	0.17	11
June	YWAR	GWY	M	ASY	58	10.5	0.18	11
June	YWAR	GBG	F	ASY	61	11.5	0.19	11.4

June	BWAR	RBR	F	SY	49	8.5	0.17	11.7
June	YWAR	BWG	M	ASY	59	11	0.19	12
June	YWAR	BWR	M	ASY	62	12	0.19	12.2
June	YWAR	RWY	M	SY	57	11	0.19	12.3
September	BWAR	GRY	U	AHY	51	7.5	0.15	9.7
September	BWAR	YGY	M	SY	52	8.5	0.16	10.6
September	YWAR	GRW	M	AHY	64	11.3	0.18	10.9
February	YWAR	GYY	F	ASY	56	9.5	0.17	9.4
February	YWAR	WYG	M	SY	59	10.5	0.18	9.4
February	BWAR	RYW	F	ASY	49	6.5	0.13	9.5
February	YWAR	YRY	M	ASY	60	10.2	0.17	9.5
February	BWAR	WRY	M	ASY	49	6.5	0.13	9.55
February	BWAR	BYY	M	AHY	47	6.5	0.14	9.7
February	BWAR	WYR	F	ASY	50	6.5	0.13	10
February	YWAR	YRG	M	ASY	59	11	0.19	10
February	YWAR	RGW	M	ASY	60	12	0.20	10.04

Appendix: Table A continued

Month	**Species**	**ID**	**Sex**	**Age**	**Wing chord/mm**	**Mass/g**	**Mass/Wing chord**	**Bill length/mm**
February	YWAR	RYG	M	SY	60	11.5	0.19	10.05
February	YWAR	WYY	M	ASY	60	9.5	0.16	10.1
February	YWAR	YYW	F	AHY	55	9	0.16	10.1
February	YWAR	YWG	M	ASY	61	10	0.16	10.25
February	YWAR	RYY	M	ASY	61	9.5	0.16	10.35
February	YWAR	YGR	M	ASY	60	11.5	0.19	10.6

February	YWAR	GYW	F	SY	60	12.5	0.21	11
February	YWAR	WGY	F	ASY	59	9.5	0.16	12
May	BWAR	GBY	M	ASY	51	7.25	0.14	9.3
May	BWAR	GRB	M	ASY	50	6.75	0.14	9.6
May	BWAR	GBW	M	SY	48	7	0.15	10
May	BWAR	RYR	M	SY	51	8	0.16	10
May	YWAR	GBR	F	ASY	60	12.3	0.20	10.05
May	BWAR	BYW	M	SY	50	7.25	0.15	10.1
May	BWAR	RBG	M	ASY	50	7.5	0.15	10.1
May	YWAR	RYB	M	SY	61	11.3	0.18	10.1
May	YWAR	GWB	F	ASY	59	10.5	0.18	10.5
May	BWAR	RBY	M	ASY	51	7.25	0.14	10.6
May	YWAR	RWB	F	ASY	58	11.3	0.19	10.8
May	YWAR	RGR	M	SY	61	10.8	0.18	11
May	YWAR	RBW	F	SY	56	10.3	0.18	11.1
May	YWAR	GWB	F	ASY	59	13.5	0.23	11.1
May	YWAR	RGB	M	ASY	63	9.75	0.15	11.3
May	BWAR	GRG	M	SY	48	7.25	0.15	11.4
May	YWAR	GWG	M	ASY	63	11	0.17	11.5
May	YWAR	RWR	U	U	61	9.75	0.16	---

Appendix: Table A

Month	Species	ID	Sex	Age	Wing chord/mm	Mass/g	Mass/Wing chord	Bill length/mm
June	BWAR	BRB	M	AHY	50	7	0.14	
June	BWAR	BRW	U	AHY	51	7.5	0.15	
June	BWAR	BYB	M	AHY	50	7.5	0.15	
June	BWAR	WBW	F	ASY	49	7.5	0.15	
June	BWAR	BGB	U	HY	49	8	0.16	
June	YWAR	BWB	M	ASY	63	11.5	0.18	
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June	BWAR	WRG	M	SY	47	7	0.15	9.8
June	YWAR	YWR	M	ASY	63	10.5	0.17	10
June	BWAR	BGY	M	ASY	51	7.5	0.15	10.1
June	YWAR	RWG	M	ASY	61	11.1	0.18	10.2
June	BWAR	BRY	U	AHY	48	9	0.19	10.2
June	BWAR	BWY	M	ASY	52	8	0.15	10.3
June	BWAR	RGY	M	ASY	49	7.5	0.15	10.4
June	BWAR	BRG	M	SY	49	8.5	0.17	10.4
June	YWAR	BYG	F	ASY	59	11	0.19	10.7
June	BWAR	BYR	M	SY	50	8	0.16	11
June	BWAR	YBY	M	ASY	50	8.5	0.17	11
June	YWAR	GWY	M	ASY	58	10.5	0.18	11
June	YWAR	GBG	F	ASY	61	11.5	0.19	11.4

Appendix: Table A continued

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June	YWAR	BWR	M	ASY	62	12	0.19	12.2
June	YWAR	RWY	M	SY	57	11	0.19	12.3
September	BWAR	GRY	U	AHY	51	7.5	0.15	9.7
September	BWAR	YGY	M	SY	52	8.5	0.16	10.6
September	YWAR	GRW	M	AHY	64	11.3	0.18	10.9
February	YWAR	GYY	F	ASY	56	9.5	0.17	9.4
February	YWAR	WYG	M	SY	59	10.5	0.18	9.4
February	BWAR	RYW	F	ASY	49	6.5	0.13	9.5
February	YWAR	YRY	M	ASY	60	10.2	0.17	9.5
February	BWAR	WRY	M	ASY	49	6.5	0.13	9.55
February	BWAR	BYY	M	AHY	47	6.5	0.14	9.7
February	BWAR	WYR	F	ASY	50	6.5	0.13	10
February	YWAR	YRG	M	ASY	59	11	0.19	10
February	YWAR	RGW	M	ASY	60	12	0.20	10.04

Appendix: Table A continued

Month	Species	ID	Sex	Age	Wing chord/mm	Mass/g	Mass/Wing chord	Bill length/mm
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February	YWAR	WYY	M	ASY	60	9.5	0.16	10.1
February	YWAR	YYW	F	AHY	55	9	0.16	10.1
February	YWAR	YWG	M	ASY	61	10	0.16	10.25
February	YWAR	RYY	M	ASY	61	9.5	0.16	10.35
February	YWAR	YGR	M	ASY	60	11.5	0.19	10.6
February	YWAR	GYW	F	SY	60	12.5	0.21	11
February	YWAR	WGY	F	ASY	59	9.5	0.16	12
May	BWAR	GBY	M	ASY	51	7.25	0.14	9.3
May	BWAR	GRB	M	ASY	50	6.75	0.14	9.6
May	BWAR	GBW	M	SY	48	7	0.15	10
May	BWAR	RYR	M	SY	51	8	0.16	10
May	YWAR	GBR	F	ASY	60	12.3	0.20	10.05
May	BWAR	BYW	M	SY	50	7.25	0.15	10.1
May	BWAR	RBG	M	ASY	50	7.5	0.15	10.1
May	YWAR	RYB	M	SY	61	11.3	0.18	10.1
May	YWAR	GWB	F	ASY	59	10.5	0.18	10.5
May	BWAR	RBY	M	ASY	51	7.25	0.14	10.6
May	YWAR	RWB	F	ASY	58	11.3	0.19	10.8
May	YWAR	RGR	M	SY	61	10.8	0.18	11
May	YWAR	RBW	F	SY	56	10.3	0.18	11.1

Appendix: Table A continued

May	YWAR	GWB	F	ASY	59	13.5	0.23	11.1
May	YWAR	RGB	M	ASY	63	9.75	0.15	11.3
May	BWAR	GRG	M	SY	48	7.25	0.15	11.4
May	YWAR	GWG	M	ASY	63	11	0.17	11.5
May	YWAR	RWR	U	U	61	9.75	0.16	---

Table A Legend

CODES

Species	BWAR	Barbuda Warbler
	YWAR	Yellow Warbler
Colour Bands	R	Red
	W	White
	B	Black
	Y	Yellow
	G	Green
Sex	M	Male
	F	Female
	U	Undetermined
Age	SY	Second Year
	AHY	After Hatch Year
	ASY	After Second Year
	U	Undetermined
	---	Bird escaped

APPENDIX II

CURRICULUM VITAE

Candidate's full name: Kevin Mahabir

Universities attended: University of the West Indies, St. Augustine, Trinidad & Tobago, BSc. 2010.

Publications: None

Conference Presentations: None