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Patterns of Seasonal Variation in Diet, Abundance, and Movement of the Scarlet Macaw (Ara macao) in southern Belize

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Department of Environmental Studies

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Patterns of Seasonal Variation in Diet, Abundance, and Movement of the Scarlet Macaw (*Ara macao*) in southern Belize

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Patterns of Seasonal Variation in Diet, Abundance, and Movement of the Scarlet Macaw (*Ara macao*) in southern Belize

by

Mark Stephen M^{c}Reynolds

A dissertation submitted in partial fulfillment

of the requirements for the degree of

Doctor of Philosophy

(Environmental Studies)

at

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DEDICATION

I dedicate this work first to the Creator of all things, who will reconcile all things back to Himself. My ultimate goal has been to do my part in that reordering with the survival of Scarlet Macaws in Belize and Central America.

Second, to the love of my life, Karen Edminster McReynolds. I could not have done this work without her cheerleading and what the King James Version of the Bible calls “longsuffering.”

Third, to my parents, Madeline Gayle Hart McReynolds, M.A., and Paul Robert McReynolds, Ph.D. Their love of God, of learning, and of travel was both taught and caught.

Also, to two Belizeans, who made my research possible. To the memory of Nicodemas Bol, also known as “Chapal,” whose untimely death in 2010, left a gaping hole in knowledge of the Chiquibul area. He showed me my first Scarlet Macaws before I had thoughts of a Ph.D. To Jeronimo Sho, former Chairman of Red Bank Village, pastor, and local macaw expert, who taught me much about Scarlet Macaws, and whose family extended warm fellowship and hospitality.

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My committee members: from Antioch University New England: Dr. Jonathan Atwood, who took me on, believed I could do this, and even visited me in Red Bank; Dr. Beth Kaplin, a model tropical ecologist; Dr. Janice Boyd from The Parrot Fund (aka Amigos de las Aves USA), an enthusiastic parrot researcher who became a patron of my work, and visited me in the Chiquibul area of Belize.

In Belize: Scott and Cheryl Stirm, for a constant second home; Ms. M. Smith at the National Meteorological Service, for weather records; Roni Martinez, Naturalist at Blancaneaux Lodge, for macaw records; Rafael Manzanero, Derric Chan, Lenny Gentle, Glenn Manzanero, Emilio Salam, Larry Santos, Carlos Rosas, Nicholas Uck, Jaime Requena, and Moises Lopez of Friends for Conservation and Development, for sightings, trail work, and lodging in the Chiquibul; Dr. Stephen Brewer, for plant identification; Tom Pop, Sipriano Canti, Jacob Marlin, and Dan Duerckson for assistance at the Belize Foundation for Research and Environmental Education in the Bladen area; Jeronimo, Seraphina, John and Celso Sho, and Cornelio Ogaldez, for knowledge of macaws, great hospitality, and local guiding at Red Bank Village; staff of the Bladen Nature Reserve for macaw records, permissions, and research assistance; Nicacio Coc and Brijilio Bolan, Belize Audubon Society staff at Cockscomb Wildlife Sanctuary, for permissions, motorcycle repair, and guiding; the late Nicodemas (“Chapal”), Celia, and Matthew Bol, and Jimmy Boucher, for Chiquibul knowledge, hospitality at Las Cuevas Research Station, and guiding; Edilberto Romero of Programme for Belize, for diligently keeping and then sharing applicable research papers; Jan Meerman of Belize Tropical Forest Studies, for GIS files, plant identification, and Biodiversity and Environmental Resource Data System of Belize (BERDS) plant and macaw records; Antonio Bol and other Jaguar Creek staff, for friendship and hospitality; Hector Mai, Forest Department Botanist, for permits, plant identification, and herbarium access; Dr. Elma Kay of the University of Belize, for assisting with the Macaw Bird Count and for plant collection methods; Marcos Cucul, guide, who first told me about macaws in Cockscomb; Jose “Pepe” Garcia of Tunich-Nah Consultants, for a tour of nest boxes on the Macal River; Paul and Zoe Walker of Wild Tracks, for information and inspiration; Dr. Marcella Kelly and Dr. Claudia Wultsch of the University of Pennsylvania, for noting macaw sightings while looking for jaguars in Cockscomb; the Shaws and staff of the Hotel Mopan in Belize City, for hospitality and motorcycle storage; Ernesto Saqui, formerly of Cockscomb, for historical information about macaws and current sightings; Sharon Matola of the Belize Zoo, for inspiration to continue the work to save the Scarlet Macaw, Belize's most beautiful bird.

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Elsewhere: In Mexico: Dr. Katherine Renton of Estación de Biología Chamela (IB-UNAM), for two interviews about her work in Belize with Scarlet Macaws, one at her research station. In England and Scotland: Dr. Owen Lewis of Oxford University, who remembered a master's thesis written long ago on Scarlet Macaws in the Chiquibul; Dr. Anthony King of Scotland, who did that first research with Nicodemas Bol, and provided his master's thesis, and who set up the wildlife sightings book at Las Cuevas; Chris Minty, formerly of Las Cuevas, for documenting the pre-Chalillo Dam era along the Macal and Raspaculo rivers.

When I was in Belize for eighteen months (two weeks there and two weeks at home) I was often in difficult conditions, alone, and in remote areas on foot. I found encouragement in three sayings when hiking solo down a trail far from help, or seeing 20 yards of mud hole of unknown depth in front of my motorcycle, or when endlessly typing. The first saying came from a teacher at Villa Colorada, Petén, Guatemala: "*Poco a poco el mono subió al coco*" (Little by little the monkey climbed the coconut tree); the second from the *Bible*, Galatians 6:9: "And let us not be weary in well doing: for in due season we shall reap, if we faint not," the third from *Celtic Daily Prayer* (The Northumbria Community 2000): "Circle me, Lord, keep protection near and danger afar."

AUTHOR PHOTOGRAPH

Mark M^{c}Reynolds, March, 2009, on the soccer field by Jeronimo Sho’s house in Red Bank Village, Belize. Guesthouse Ridge is in the background. Normal procedure was to wear a helmet and large pack, with gear strapped to the back rack as well. Distance traveled by motorcycle (125cc) was 18,656 km (11,592 miles) on dirt and paved roads. Photo by Karen M^{c}Reynolds.

ABSTRACT

Patterns of Seasonal Variation in Diet, Abundance, and Movement of the Scarlet Macaw (*Ara macao*) in southern Belize.

This study was conducted in 2008 and 2009 to determine if Scarlet Macaws (*Ara macao*), in subtropical southern Belize, Central America, are seasonal and elevational migrants and if their movement is influenced by seasonally abundant food. Reports from southern Belize indicated strongly seasonal sightings of macaws ($N \approx 200$) in two separate areas of considerable difference in elevation. I monitored plant phenology plots (2 m x 500 m) in low ($N = 6$) and high ($N = 6$) elevation areas for a year to compare fruit abundance with macaw sightings in point counts on the plots and nearby. My point count data and historical sightings indicate strongly seasonal patterns of macaw movement between the low eastern foothills of the Maya Mountains, notably at Red Bank Village, and the higher Chiquibul area to the west, over the Maya Mountains. Other researchers have recorded macaw flights over the Maya Mountains. In the Chiquibul, their high-elevation breeding grounds, my sightings of macaws occurred year-round, but dropped at the beginning of the breeding season in January. At that time, sightings of likely non-breeders rose in low-elevation areas, peaking in February and March with abundant *Sloanea tuerckheimii*, *Pera arborea*, and *Xylopia frutescens*. At that elevation, no macaws were sighted from April through November. At Red Bank, ripe *X. frutescens* was strongly correlated with Scarlet Macaws; the abundance of both dropped to zero by April. Fruit availability peaked in the Chiquibul in May, whereas macaw sightings peaked in June and dropped in July; low numbers of macaws were sighted in August, September, and October. I reviewed the natural history of Scarlet Macaws in Belize and determined that they have a generalist diet, numerous natural limiting factors, and limited populations and distribution due to habitat destruction and the pet trade. In response, I am advocating for anti-poaching efforts and new protected areas in Belize. The electronic version of this dissertation is freely available in the open access OhioLINK ETD Center (http://etd.ohiolink.edu).

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INTRODUCTION

Parrots, with 356 species worldwide (Forshaw 2006), contribute to the biodiversity of tropical ecosystems. Because of loss of habitat and nest poaching for the pet trade, many parrot species are at risk of extinction worldwide (Forshaw 2006; Forshaw & Knight 2010); members of the parrot family are more liable to become extinct than any other bird family (BirdLife International 2000) and have experienced dramatic drops in population (Butchart et al. 2004). Of the 140 parrot species in the Neotropics, 42 are vulnerable to extinction and the 98 non-threatened species are almost all experiencing population declines (Collar & Juniper 1992). In Central America, the pet trade, deforestation, and hunting have decimated Scarlet Macaw numbers (Snyder et al. 1999) and the species is listed in CITES' Appendix 1, which highly restricts its international trade (CITES 2011).

In Central America, the Scarlet Macaw is locally known as *lapa roja* (Nicaragua & Costa Rica), *guara roja* (El Salvador & Honduras), *guacamaya roja* (Guatemala & México), and Macaw Parrot or Scarlet Macaw (Belize). Scarlet Macaws historically occurred from southern Mexico through Panama (Ridgely 1983). The Scarlet Macaw includes two subspecies, *Ara macao macao* and *A. m. cyanoptera* (Wiedenfeld 1994), with genetic work confirming the split (Schmidt & Amato 2008, 2009); there are also haplotype differences between populations of *A. m. cyanoptera* (Feria & de los Monteros 2007a; Schmidt & Amato 2008, 2009). Wiedenfeld (1994) posited that *A. m. cyanoptera* occurred from Central Nicaragua to Mexico, with a gradation zone for the two subspecies in central Nicaragua south to Costa Rica, but the boundary between the two subspecies is now considered to be near the Nicaragua and Costa Rica border (Schmidt & Amato 2008) with *A. m. macao* continuing through Panama and into South America. Because of the widespread distribution and relatively high population numbers of *A. m. macao* in South America, the entire species is listed as a "species of least concern" (BirdLife International 2011), although *A. m. cyanoptera* was reported by Wiedenfeld (1994) to be perilously close to extirpation in Central America and the situation has not improved. Distribution of both *A. m. macao* and *A. m. cyanoptera* within Central America and Mexico, pre- and post-1980, is shown below (Figs. 1, 2).

Scarlet Macaw distribution within Central America and Mexico is spotty. *A. m. cyanoptera* was reported to be very rare in Honduras and Nicaragua (Wiedenfeld 1994), but Scarlet Macaws are reported

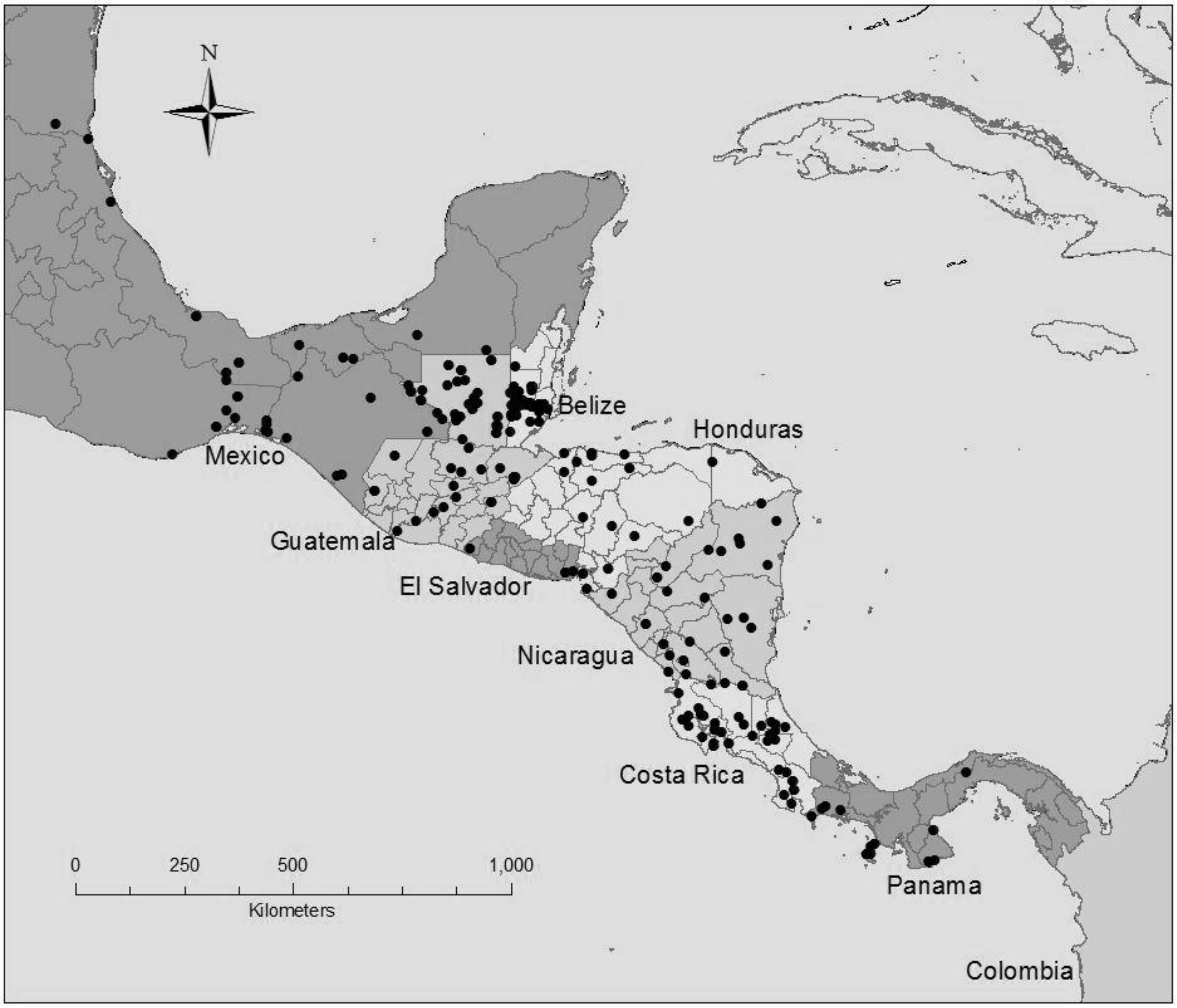


Figure 1. Scarlet Macaw distribution in Central America and Mexico before 1980. Points represent one or more Scarlet Macaw sightings. Sightings data from literature (*N* = 321); see Appendix A for sources.

to be common in the relatively unstudied Moskitia (Mosquitia) area of Honduras (Anderson et al. 2004); recent research indicates a viable population there (Portillo Reyes 2005; Portillo Reyes et al. 2010b). Groups exist along the Rio Platano (Anderson 1998; Gallardo 2009) and Rio Patuca (Global Travel Club 2010; Bonta, pers. comm. 2006). Scarlet Macaws occur in eastern Nicaragua (Howell 1972; Martinez-Sanchez 1991a, b) and a remnant population exists on a western volcano (Martinez-Sanchez 1991a, b; Tellez & Rodriguez 2006). They were reported to have been extirpated from El Salvador (Komar & Dominguez 2001), although recent sightings have been reported at La Unión and Jiquilisko, El Salvador, said to be from birds reintroduced at Isla Zacate Grande, Honduras (Gilardi 2012). Small, isolated populations have been reported in Mexico and Guatemala (Iñigo-Elias et al. 2001; Boyd & McNab 2008),

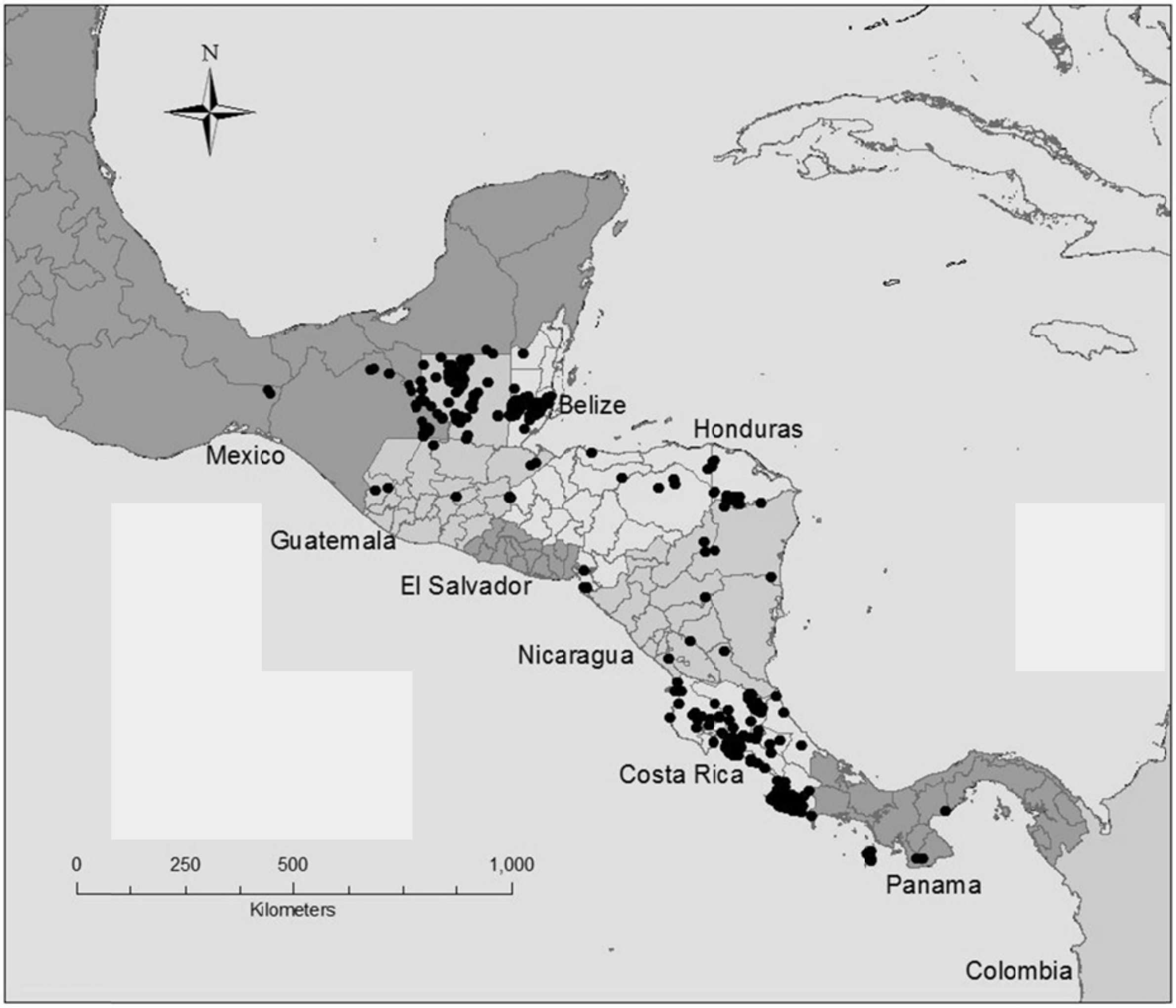


Figure 2. Scarlet Macaw distribution in Central America and Mexico after 1980. Points represent one or more Scarlet Macaw sightings. Sightings data from literature (*N* = 2993) and my observations; see Appendix A for sources.

in Costa Rica (Vaughan et al. 2005) and in Panama (Ridgely & Gwynne 1989). Population estimates for *Ara m. cyanoptera* and *A. m. macao* from Mexico to Panama are shown in Table 1.

Scarlet Macaws are considered “endangered” in Belize (Meerman 2005a). The small population in Belize, approximately 200 by my field estimates, faces large threats from Guatemalans who regularly cross into Belize to poach chicks and shoot adults (Britt 2010d; Groff 2011). Unprotected habitat (Meerman 1999; pers. obs. 2007-2009) and hurricanes (Matola, unpub. 1998), plus occasional hunting (Romero, pers. comm. 2006) and nest poaching (Duerckson, pers. comm. 2009) by Belizeans round out the problems confronting this species. Two additional related threats compound the others: lack of basic information about the species and absence of a carefully formulated conservation management plan.

Table 1. Population estimates for *Ara macao cyanoptera* and *A. m. macao* from Mexico to Panama.

Country	Population Estimate	Subspecies
Mexico	137 individuals, Boyd & McNab (2008). “Unknown #”, SEMANARP (2009).	*cyanoptera*
Guatemala	≈ 150-250 individuals, Boyd & McNab (2008).	*cyanoptera*
Belize	≈ 200 individuals (M. M^{c}Reynolds).	*cyanoptera*
El Salvador	0 individuals, Bjork & Komar (2008).	*cyanoptera*
Honduras	1000-1500-plus individuals, by MMc analysis of Portillo Reyes et al. (2004).	*cyanoptera*
Nicaragua	764 individuals maximum, Lezama (pers. comm. 2010).	*macao* & *cyanoptera*
Costa Rica	≈ 1800 individuals maximum, via compilation of Arias et al. (2008), Dear et al. (2005b), Guzman (2008), Penard et al. (2008).	*macao*
Panama	≈ 100 individuals, Keller & Schmitt (2008)	*macao*

Before effective bird conservation and management can occur, information must be gathered on life history, ecology, range, and distribution, as well as demographics (Sutherland et al. 2004). Although some basic information on the abundance and ecology of Scarlet Macaws is available for Mexico and Central America, my work focused on patterns of seasonal variation in diet, abundance, and movements of this species in southern Belize. My research was prompted by a need to know where these macaws are during different times of the year. Anecdotal evidence suggested a strong possibility of seasonal and elevational movements, with large numbers of macaws seen in the lower eastern foothills of the Maya Mountains, specifically near Red Bank Village, during the dry season, contrasting with absence of observations in the wet season. In the higher-elevation Chiquibul area to the west and over the Maya Mountains, some macaws were seen year-round, but with high concentrations during the wet season, May to October, when they were absent from Red Bank and other low-elevation areas. I resolved to see if these seasonal concentrations were caused by movements amounting to migration. I wanted to explore possible factors associated with such behavior, thereby contributing to a conservation management plan. Data collected from my own field work, combined with the compiled sighting records of others, suggest that elevational migration of Scarlet Macaws in southern Belize is associated with seasonal variation in diet.

LITERATURE REVIEW

PLANT PHENOLOGY

Among environmental factors influencing bird migration, the one that stands out is food availability. Migrant birds tend to leave areas of low food availability and go to areas of high food availability (Ketterson & Nolan 1983). Migration is such a phenological phenomenon that birds predictably arrive on their breeding grounds within the same weeks every year, barring some stochastic event, and their arrivals coincide with the presence of sufficient food for reproduction. Food availability is also a phenological phenomenon, changing throughout the year.

The 23.5° tilt of the Earth and its annual rotation around the sun produce seasons that are more evident at the higher latitudes. At the equator, day is 12 hours, as is night, but as one moves north or south, the length of day varies with latitude and season. The amount of irradiance or insolation received per unit of area also varies (Strahler & Strahler 2002). Plants, dependent on sunlight to photosynthesize, have adapted leaf drop, leaf flush, flowering, and fruiting to the amount of insolation, photoperiod, and climate (especially rainfall), which change at different latitudes as the Earth rotates.

Phenological studies indicate that insolation peaks coincide with peaks of leaf flushing and flowering (van Schaik et al. 1993). In a comparative study of eight tropical forests, leaf and flower production was observed to accompany peaks of insolation occurring on a seasonal basis (Wright & Schaik 1994). To study the impact of water availability or rainfall, bud break in individuals of two tree species was observed and found to be synchronous between creekside and dry-sited individuals; the authors concluded that photoperiod appeared to be the major factor behind bud break (Borchert & Rivera 2001).

Extended periods of alternating dry and wet seasons become more pronounced as one moves away from the equator. Tropical forests have adapted to the seasonal change in precipitation. Within Central America the dry season starts slowly in November or December, becoming cooler in the north. It ends at a fairly predictable date by region, as more rain produces much new plant growth and swarms of insects (Janzen 1967). An overextended dry season, or one with subnormal rainfall, can produce significant mortality in tropical forests (Condit et al. 1995). Leaf drop in the dry season is common in dry tropical forests (Frankie et al. 1974). Although leaf drop has been hypothesized to be a function of water loss, in one experiment almost all species still dropped leaves despite regular watering and with little delay (Wright & Cornejo 1990). Flowering of trees peaks during the dry season in Central America (Janzen 1967; Croat 1975; Lobo et al. 2008), particularly in dry forest regions (Frankie et al. 1974). This peak may occur because the trees are capable of storing water in the dry season, pushing out new leaves at a time of highest insolation, and both leaves and flowers at a time when insects are few because of minimal moisture (Wright 1996). Losing transpiring leaves may enable trees to have enough water to flower and grow new leaves later (Borchert 1983). Changes in rainfall can trigger leaf flush at the beginning of the wet season and start a plant's flower and fruit production (Frankie et al. 1974; Bullock & Solis-Magallanes 1990; van Schaik et al. 1993; Lobo et al. 2008). For some plants, leaf flush is decoupled from the production of flowers and fruit; in other species leaf growth and flowering are concurrent (Borchert 1980, 1983). On the other hand, much of the synchronous bud break and flowering that occurs may be the result of seasonal variation in insolation (Calle et al. 2010); in January and February, Belize can be awash in yellow and red tree blossoms, making some valleys and hillsides look like New England in the fall.

Seasonal phenological variation results in differing amounts and quality of food resources throughout the year, requiring consumers to adapt through "dietary switching, seasonal breeding, changes in range use, or migration" (van Schaik et al. 1993). Seasonal food switching among frugivores and folivores is found in primates (Silver 1992; Kaplin et al. 1998; Furuichi et al. 2000; Kaplin 2001) and other vertebrate herbivores such as rodents and ungulates; they must eat (or store) what is seasonally available. Large frugivorous Central American birds that seasonally switch foods include guans (Cracidae), several quetzals and trogons (Trogonidae), bellbirds (*Procnias* spp.), and umbrellabirds (*Cephalopterus* spp.), as well as various parrots and macaws. Fruit size and shape are important (Gautier-Hion et al. 1985). Among frugivorous birds, bill gape determines the largest fruits that they will eat (Wheelwright 1985). Large species, such as cotingas (Cotingidae) and toucans (Ramphastidae), eat both large and small fruits, including larger lipid-rich fruits, but smaller species stick to smaller carbohydrate-rich fruits (Moermond & Denslow 1985).

Plant reproduction depends on seed production. The "seed shadow" effect (Willson 1993) makes seeds more likely to germinate and live to reproductive age when they are far from the parent tree. Under the tree, competition with the parent tree for sunlight, water, nutrients (Howe 1980), and destruction by fungi (Bagchi et al. 2010) cause significant density-dependent mortality. A recent study found a strong correlation between mortality and a combination of shade tolerance and conspecific density (Kobe & Vriesendorp 2011). Small, light seeds are carried away by the wind; heavier seeds depend on a fruit attractant to entice larger animals to transport them. When a frugivore consumes fruit, the seed may not be destroyed but may be deposited some distance away from the parent tree in fecal matter.

Many frugivorous animals are seed dispersers. Mammalian seed dispersers are opossums (*Philander opossum*) and (*Didelphis marsupialis*), tapir (*Tapirus terrestris*), agouti (*Dasyprocta punctata*), spiny pocket mouse (*Heteromys desmarestianus*) (Forget & Milleron 1991; Medellin 1994; Brewer & Rejmanek 1999; Fragoso et al. 2003), and various primates (Howe 1980; Chapman 1989; Kaplin & Moermond 1998; Andresen 1999, 2001, 2002; Vulinec 2002; Riba-Hernández et al. 2003; Wehncke et al. 2004; Gross-Camp & Kaplin 2005). Birds are well-known seed dispersers (Howe 1977; Howe & Kerckhove 1979; Wheelwright 1983; Wenny & Levey 1998; Whitney & Smith 1998; Yumoto 1999; Holbrook et al. 2002; Carlo et al. 2003; Pejchar et al. 2008). Insects are also seed dispersers (Andresen 1999, 2001, 2002; Oberrath & Böhning-Gaese 2002; Ness et al. 2004). Fig seeds are dispersed by some 1274 bird and mammal species that consume the fruit; a major fig-eating family is Psittacidae (Shanahan et al. 2001).

Fruit is important in the diet of many parrots (Juniper & Parr 1998), which often seek the seed, making them significant seed predators (Howe 1980; Jordano 1983; Moermond & Denslow 1985; Galetti & Rodrigues 1992; Galetti 1993; Renton 2001; Francisco et al. 2002; Ragusa-Netto 2002, 2005; Diaz & Kitzberger 2006; Ragusa-Netto 2007a; Boyes & Perrin 2010; Villasenor-Sanchez et al. 2010). Even small fig seeds (*Ficus* sp.) are cracked and digested (Olson & Blum 1968; Janzen 1981).

BOTANICAL STUDIES IN BELIZE

Belize has high plant diversity: 3408-plus species (Balick et al. 2000), and no published flora with keys, but I found two extensive online databases and a book with data on plant specimens from Belize (Balick et al. 2000; New York Botanical Gardens 2007; Tropicos.org 2010). The first “ecosystem” map was a countrywide soil survey that also included plant assemblages (Wright et al. 1959); it served as a base for a later vegetation-mapping effort (Iremonger & Brokaw 1996). More recently an extensive GIS-based ecosystem classification scheme and map for Belize has been produced, with less than a 0.8 ha (2 acre) resolution (Meerman & Sabido 2001); it follows UNESCO ecosystem codes, and uses the same methodology as the Central America Ecosystems Map (World Bank and CCAD 2001; Vreugdenhil et al. 2002), of which it is a part. This Belize ecosystem map was constructed via remote sensing techniques and much of it has been “ground-truthed” via fieldwork (Meerman, pers. comm. 2004). The most current GIS-based macro-scale vegetation classification and map for the Maya Mountains in Belize (Penn et al. 2004) is incorporated into the Belize ecosystem map (Meerman, pers. comm. 2004), but differences remain. Most of my study area is covered by both maps, but the eastern sites of Red Bank and Bladen were covered only by Meerman and Sabido (2001). Important botanical works include Bridgewater et al. (2006a) and Brokaw (1991) for the Chiquibul region, Brewer et al. (2003) and Brewer and Webb (2002) for the Bladen Nature Reserve, Meerman (1999, 2002) for Red Bank Village, and Kamstra (1987), and Silver (1992) for Cockscomb Basin.

Plant phenology work is rare in Belize. I found only one phenological study of plants in Belize, in the drier and northern Rio Bravo area, out of my study area (Hess 1994). An incomplete draft document containing phenological notes is in circulation focused on the Chiquibul, possibly authored by M. G. Penn, the English botanist who mapped vegetation in the Maya Mountains (Penn et al. 2004). This document lists 88 species, partially noting month of leaf loss, flowering, and fruiting. In my study area some phenology work on macaw-foods was begun at Red Bank and further research proposed via a fruit trail monitored by villagers (Meerman 2002). The fruit trail idea was abandoned as too complicated for villagers and the work was not compensated, a disincentive (Romero, pers. comm. 2006). Research on how black howler monkeys (*Alouatta pigra*) make seasonal use of plants was done in the Cockscomb Wildlife Sanctuary by Silver (1992).

With no published flora for Belize, I used the following literature for identification and phenology data: Standley & Record (1936); Wright et al. (1959); Pennington & Sarukhan (1968); Gentry (1993); Miller (1995); Joseph et al. (1998); Balick et al. (2000); Smith et al. (2004); Zuchowski (2005); Bridgewater et al.(2006a); Brokaw et al. (2007).

SCARLET MACAWS IN BELIZE

Abundance Estimates

In Central America, the pet trade, deforestation, and hunting have decimated Scarlet Macaw numbers (Wiedenfeld 1994; Snyder et al. 1999), so that Enkerlin-Hoeflich et al. (1999) concluded that "Within the next 10 years, all middle American populations will probably disappear except for those in highly protected (i.e., guarded) areas."

Determining abundance of Scarlet Macaws in Belize has been difficult due to their low numbers and remote habitat. Two studies agreed that the overall population in Belize was only a few hundred individuals (Mallory 1994; Renton 1998a, 1998b); another specified 60-100 (King 1998a). Romero (2004) estimated 150 individuals at Red Bank in January 1999. Enkerlin-Hoeflich et al. (1999) determined the species deserved "special conservation concern." Sixty to 100 individuals were estimated again (Minty 2001), in a study focused only on the area affected by the Chalillo Dam. According to Jones & Gardner (2003), macaw numbers "may not exceed 150" individuals. One day's count in 2004 tallied a total of 219 individuals from four widely separated sites in the Chiquibul area (Bol, pers. comm. 2005). A WCS-Guatemala estimation, based on my field observations, puts the Belize population at 105 (Wildlife Conservation Society - Guatemala 2005) or 103 (Boyd & McNab 2008).

Diet Studies

Since lack of food or lack of habitat protection may pose a threat to the survival of Scarlet Macaws, it is important to know which species of plants are eaten by these birds. One of the first food studies in Belize reported that quamwood (*Schizolobium parahyba*), a leguminous tree and so presumably protein-rich, was a key component of nestling diet and often used for nesting (Matola & Sho 1998; Renton 1998b, 2006). See Table 2 for food items for two Scarlet Macaw nestlings. Other foods reported eaten in the Red Bank area with regularity, but on a seasonal basis, included fruit from these trees: polewood (*Xylopia frutescens*), wild annatto (*Sloanea tuerckheimii*), and mo tree (*Pera arborea*); the latter was previously thought to be *P. barbellata* (Meerman 1999, 2002). Most feeding observations, including those of Renton (2006), occurred during the breeding season, within the dry season, and at Red Bank or in the general areas of the Chiquibul Forest Reserve and National Park or on the Raspaculo Branch.

Table 2. Food for two macaw nestlings May 17-22, 1998, on the Macal River, Belize. Data from Renton (1998b, 2006).

Food Item	**% Frequency**	**% Biomass**
Cnidoscolus ssp.	100	66
Schwartzia ssp. Likely *Swartzia* spp.*	66.7	24
Schizolobium parahybum *S. parahyba**	100	12
Wood Chips	66.7	6
Sebastiana longicuspis *Pleradenophora longicuspis**	33.3	1
Insect Larvae	33.3	0.9

* Correction or addition by MMc

Anthropogenic Limiting Factors

In Central and South America, Scarlet Macaws have experienced habitat destruction and poaching (Snyder et al. 1999), as have other Neotropical parrots (Wright et al. 2001). The government of Belize claims that it is the country least affected by habitat destruction in Central America, with approximately 82% of the land forested and 37% of the land under some form of protection (Sabido 2001). Most of the forest is second growth, because Belize's early economy was founded on wood exports (Standley & Record 1936; Bolland 1977); much of the remaining forest has been impacted by hurricanes (Meerman, pers. comm. 2005). The Land Information Center, a branch of the Belizean government, concluded that 781 km^2 of forest, or 3.5% of the country's total land area, was cleared from 1989 to 1994 (Casteneda 1998). By analysis of satellite imagery, Cherrington et al. (2010) found an annual deforestation rate of 0.6% during 1980 - 2010, with the national percentage of forested land dropping from 76% to 63%.

In the largely unprotected Toledo District, Emch et al. (2005) described a 10% forest loss due to agricultural expansion from 1975 to 1999; Sho (pers. comm. 2009) stated that macaws have been extirpated from the southern part of that district. In Stann Creek District, extensive logging, which eliminated possible macaw nest trees and allowed hunters easy access via logging roads, occurred in the eastern basin of what is now the Cockscomb Wildlife Sanctuary during the 1960's and from 1979 to 1980 (Saqui, pers. comm. 2009). In what is now Chiquibul National Park and Chiquibul Forest Reserve in Cayo District, Bird (1998) reported extensive logging that included quamwood. The Belizean Forest Department still permits selective logging in the Chiquibul Reserve; in 2009 I observed selective second cuts of nargusta (*Terminalia amazonica*) and cedar (*Cedrela odorata*) during the dry season near San Pastor.

Poaching is the most immediate problem for Scarlet Macaws in Belize (Britt et al. 2011; Groff 2011), but Belizeans are rarely involved in poaching. Poachers are almost always Guatemalans who are illegally in Belize to harvest *xate* (Britt et al. 2011; Groff 2011; pers. obs. 2009), which is one of three palm species (*Chamaedorea ernesti-augustii, C. oblongata, C. elegans*), and estimated to be worth five million dollars in my study area (Bridgewater et al. 2006b). The Guatemalans, called *xateros*, may spend a week or two cutting *xate* in the Chiquibul National Park or Forest Reserve and then bring the *xate* to Guatemala (FCD Rangers, pers. comm. 2009); from there the *xate* goes to international floral markets (Valle et al. 2000). While harvesting *xate*, Guatemalans also poach Scarlet Macaw chicks, and any other wildlife they may find (Bridgewater et al. 2006b; 7NewsBelize.com 2009; Groff 2011). The Chiquibul area is heavily impacted by *xateros* (Hicks et al. 2011); 89% of nests monitored along the Macal and Raspaculo rivers were poached in 2011 (Britt et al. 2011).

Previous Macaw Observations and Distribution

No observations have encompassed the entire distribution of Scarlet Macaws in Belize nor have there been any year-round studies of these birds. The eastern foothills of the Maya Mountains were largely ignored in favor of studies along the Macal and Raspaculo rivers and near Las Cuevas Field Station, all in the Chiquibul. Previous studies of macaws were largely exploratory, some incidentally mentioning Scarlet Macaws (Kamstra 1987; Barlow & Caddick 1989; Kainer 1990; Mallory 1991; Matola & Sho 1998; Meerman 1999; McRae 2000; Matola & Sho 2002b).

More systematic studies along the Macal and Raspaculo rivers included point counts (Minty 2001), point counts and flight direction mapping (Mallory 1994), and diet and behavior observations at two nests (Renton 1998a, 1998b, 2006). Systematic work was also done in the Las Cuevas area (Bol & King 1996; King 1998a, b). Checklists, status reviews, and country-wide environmental reports have focused on macaws in the Chiquibul (Russell 1964; Hartshorn et al. 1984; Wood et al. 1986; Manzanero 1990; Clinton-Eitniear 1991; Manzanero 1991; Wiedenfeld 1994; Enkerlin-Hoeflich et al. 1999).

Early records of Scarlet Macaws in Belize are summarized (Fig. 3), with the majority in the Cayo District. The first published account of Scarlet Macaws in Belize comes from an expedition into the Chiquibul and Mountain Pine Ridge areas of the Cayo District. Shortly after leaving San Antonio Village and coming into the Mountain Pine Ridge area, Fowler (1880) wrote, "An armadillo was killed, and except for macaws and hawks, no other sign of life appeared." Reliable accounts locate Scarlet Macaws in the 1940’s in the August Pine Ridge and Gallon Jug areas of Orangewalk District, where they were sought for pets (Urbina, pers. comm. 2010), and in Pueblo Viejo Village in the far southern part of the Toledo District (Sho, pers. comm. 2009). In the 1950’s macaws were seen in the Cockscomb Basin area, Stann Creek District (Kamstra 1987). The first and only Scarlet Macaw specimen was collected from the Macal River at Ballerina Camp, Cayo District, on April 22, 1955 (LSUMZ 20535). Groups of Scarlet Macaws were seen in the Hummingbird Highway area of Caves Branch and Ringtail in Cayo District before Hurricane Hattie, approximately 1961 (Scott, pers. comm. 2008). Russell (1964) wrote:

> Flocks of a few to 30 macaws frequent the uninhabited headwaters of many of the larger streams in the central part of British Honduras. I have seen “guacamayas”, as they are called locally, in the Mountain Pine Ridge, along the Eastern Branch of the Belize River, near the Hummingbird Highway, and in the upper parts of South Stann Creek. They ascend to 3000 feet or more in the Cockscomb Mountains; and in late May 1959, I saw a pair of macaws attending what I suspect was an occupied nest in a tall tree on the crest of a narrow ridge south of Victoria Peak. In the Mountain Pine Ridge, flocks are sometimes observed in pine trees a short distance from the rainforest. Macaws, to my knowledge, do not enter the coastal plain in British Honduras, although escaped cage birds have been seen near Belize [City].

Reports of Scarlet Macaws have also come from the southern coastal plains. Mallory and Matola (2002) noted that:

> Dora Weyer (Pers. com.) reported that Scarlet Macaws used to occur in the coastal pines east of the [Maya] mountains. Charles Wright (Pers. comm.) reported that every April in the 1970’s a few pairs flew in from the southwest to the Big Falls area (Toledo District) apparently to breed in a stand of gigantic pines near the Rio Grande River. After the stand was cut in 1985-86 the birds no longer returned.

In 1978 Scarlet Macaws were seen flying downstream in the afternoon from the Hawksworth Bridge in San Ignacio (Matola and Russ; pers. comm. 2010). By 1986 the bird was described as uncommon and reported only from the Chiquibul (Wood et al. 1986).

AVIAN MIGRATION

Avian movements are described in six intergrading typologies (Newton 2008, 2010). Local movements exhibit spatial patterns as when Scarlet Macaws move daily between roosting and foraging areas. Dispersive migration describes one-way movements in which the young leave their natal territories, ultimately to establish their own territories and pair bonds (Atwood, pers. comm. 2012). Another definition of dispersive migration includes seasonality, regular movements to and from the breeding area, and may include “altitudinal migration” up or down a mountain as a subset (Berthold 2001). The term “altitudinal migration” is often used synonymously with “elevational migration”; I use “elevational migration” because birds are located at elevations, and altitude is more often used in conjunction with height in an aerial sense. A broader definition of elevational migration is any movements that create a “change in the population’s centre of gravity” (Newton 2010). As most often used, “migration” refers to annual, often long-distance movements in which an entire population moves in a spatially and temporally predictable manner between breeding and nonbreeding areas (Berthold 2001). Irruptive movements are related to irregular prey populations and weather, and nomadic movements are ascribed to birds that never exhibit regular breeding territories.

Partial migration occurs when some individuals or populations of a species migrate, while others do not (Terrill & Able 1988); it is common in birds (Lundberg 1988), and can exist in the context of other migration strategies such as elevational migration (Newton 2010). Partial migration has obligate and facultative forms (Schroeder & Braun 1993), resulting in movements that may spatially and temporally vary from individual to individual and from year to year (Berthold 2001; Boyle 2008c; Newton 2010; Boyle 2011).

Several hypotheses that try to explain partial migration focus on competition for food or breeding territory (Lundberg 1987, 1988; Kaitala et al. 1993). The dominance hypothesis, applied to elevational migration, posits that older or larger birds outcompete younger and smaller birds, which migrate elsewhere to better food circumstances in lower-elevations (Ketterson & Nolan 1976). The body-size hypothesis, when applied to elevational migration, posits that poor weather in high-elevation breeding areas negatively impacts foraging ability so that larger individuals are favored because they are more capable of prolonged fasting (Ketterson & Nolan 1976). An arrival-time hypothesis focuses on the

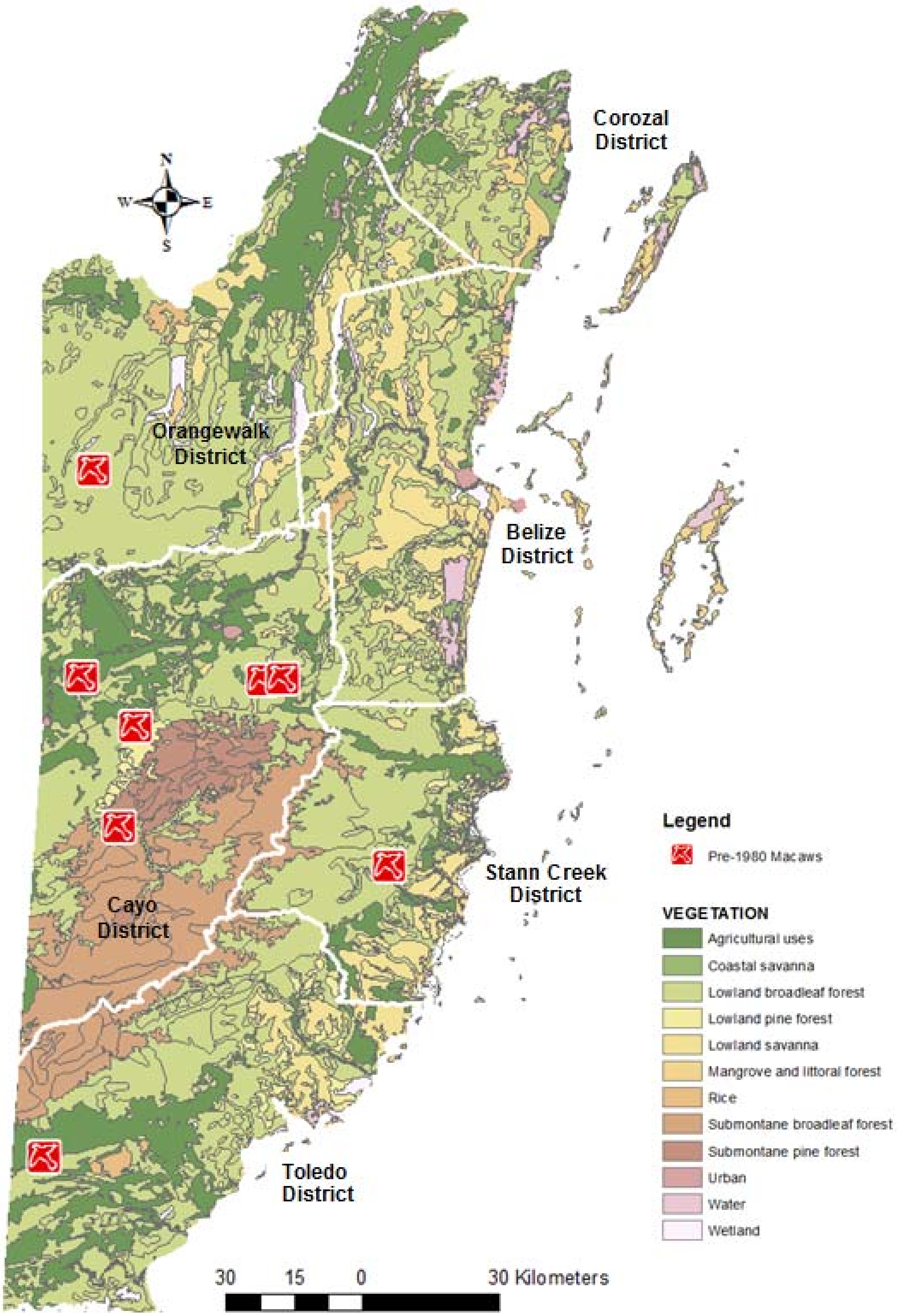


Figure 3: Distribution of pre-1980 records of Scarlet Macaws in Belize. Points in Belize refer to unique location records (N = 8), five are approximations. See Appendix B for sources of Scarlet Macaw records. Vegetation map by Meerman & Sabido (2001).

reproductive advantage for birds that stay on the breeding grounds because they can succesfully compete in conditions of food scarcity found there (Ketterson & Nolan 1976; Kokko 1999).

Explanations of elevational migration have typically revolved around food, with species moving in response to seasonal changes in fruit and flower availability (Wheelwright 1983; Stiles 1988; Blake & Loiselle 1991; Loiselle & Blake 1991b; Levey & Stiles 1992). Regular elevational migration by large frugivores, in particular, has been shown to correlate with seasonal fruit abundance (Wetmore 1972; Stiles et al. 1989; Powell & Bjork 1995; Chaves-Campos et al. 2003; Powell & Bjork 2004; Papes et al. 2012). Other authors, however, have suggested that seasonal fluctuations in fruit availability are only a partial explanation for elevational migration (Rosselli 1994; Chaves-Campos 2004; Boyle 2006; Boyle et al. 2011). For example, Boyle (2008a) and Papes et al. (2012) believe that elevational migration may be associated with avoidance of predation, and Boyle et al. (2010) and Ramos (1983) mention storm-related elevational movements.

Elevational migration of frugivores is common in Central America (Wheelwright 1983; Stiles 1988; Loiselle & Blake 1991b; Powell & Bjork 1995; Boyle 2011). Wheelwright (1983) described Resplendent Quetzal (*Pharomachrus cinnoa*) “between-habitat movements [in Costa Rica and involving elevation change] corresponded predictably to the phenology of the Lauraceae.” Powell and Bjork (1995) confirmed quetzal dependence on Lauraceae, but showed no plant phenology work, assuming that quetzals tracked their food in different habitats and elevations. In Mexico, quetzals were elevational migrants, but the authors reported no correlation of quetzals with Lauraceae species or with fruit abundance on an annual basis (Solorzano et al. 2000); one of their graphs, however, appears to show some positive correlation for both during the breeding period.

The Bare-necked Umbrellabird (*Cephalopterus glabricollis*), a large frugivore, is an elevational migrant, breeding at high elevations in Costa Rica and migrating to lower areas (Chaves-Campos et al. 2003). The authors concluded that these birds may be partially dependent on the seasonal abundance of food at the highest and lowest elevations.

Observations of the Three-wattled Bellbird (*Procnias tricarunculatus*) also showed elevational migration (Skutch 1969; Wetmore 1972; Stiles et al. 1989) and Lauraceae was also important to these birds (Skutch 1969; Wheelwright et al. 1984). Powell and Bjork (2004) found a complex elevational migration in this bird and noted that two species of Lauraceae were the primary food for three to four months. Using remote sensing, and analysis via ecological niche models, Papes et al. (2012) predicted the presence of this bird in Costa Rica at Corcovado, but not at Monteverde, where it is found.

A study in Costa Rica of resident large frugivorous birds found some evidence of elevational movement due to foods: “birds in the highlands and lowlands partially overlapped with periods of high fruit abundance at those elevations.” Fruit presence was one factor driving this elevational migration; it was not a signal to migrate to the lower areas, but did influence these birds to move upslope (Chaves-Campos 2004). Similar findings occurred in work with White-ruffed Manakins (*Corapipo altera*) (Boyle 2010).

SEASONAL MOVEMENT BY PARROTS AND MACAWS

Food Tracking and Seasonality of Diet

Few parrots are migratory in a classical sense, but many make “partial, dispersive, nomadic, irruptive, irregular, or local movements” in response to the changing availability of tropical food resources (Collar 1997). Juniper and Parr (1998) state that parrots are “neither sedentary nor migratory but mobile within a geographic area.” Forshaw (2006) mentions another parrot movement possibility of “seasonal shifts in altitudinal range.” Parrots make daily movements in search of food (Marsden et al. 2000; Evans et al. 2005), but some also make extensive seasonal movements in search of food. The flowing examples show that extensive seasonal or annual movement is not rare among parrots and macaws, and that such movement can often be tied to seasonal production of food.

Seasonal movements of parrots have been noted in Australia and Tasmania (Dreschler 2000; Mac Nally & Horrocks 2000; Donaghey 2003; Manning et al. 2007; Davis et al. 2012), and some Afro-Asian parrots are elevational migrants (Juniper & Parr 1998). In South America and the Caribbean, some parrots have been found to be seasonal migrants (Krabbe 2000; Stahala 2008; Marini et al. 2010).

Seasonal movements of parrots that mirror changes in food abundance have been seen in Africa (Symes & Perrin 2003b; Boyes & Perrin 2010), in Central America and Mexico (Renton 2001; Snyder & Russell 2002; Bjork 2004; Bonilla et al. 2010), and in South America (Bonadie & Bacon 2000; Diaz & Kitzberger 2006; Ragusa-Netto 2007c), with two studies including Scarlet Macaws (Moegenburg & Levey 2003; Cowen 2009).

Macaw movement has been tied to seasonally abundant food. One 15-year study in Ecuador stated that “the relationship observed between parrot abundance [including Scarlet Macaws] and fruit abundance implies that parrots are quite successful in tracking fruit resources in time and space” (Sosa-Asanza 2002). In Costa Rica and Nicaragua, the Great Green Macaw (*Ara ambiguus*) has distinct breeding and feeding areas (Bjork & Powell 1999; Chassot & Arias 2002), moving to track a major seasonal food item (Monge et al. 2003); movements in Ecuador are also influenced by seasonal food availability (Berg et al. 2007). Red-bellied Macaws (*Ara manilata*), Scarlet Macaws, and Red-and-green Macaws (*Ara chloroptera*) are seasonally abundant in Ecuador and make “large-scale, seasonal movements across habitat types” (Karubian et al. 2005).

In the Manu Biosphere Reserve of southeast Peru, a survey of large macaws, including Scarlet Macaws, showed low numbers in the dry season and a threefold increase in the rainy season, suggesting seasonal dependence on food resources and that these macaws track food sources (Renton 2002). On the other hand, a four-year study in the same region saw little seasonal difference in combined sightings of Scarlet Macaws and Red-and-green Macaws (Pitman et al. 2011). Clay-lick use in Manu declines when parrots and macaws, including Scarlet Macaws, move to other sites, presumably for seasonally available food (Brightsmith 2004a).

Scarlet Macaws are known to do “some local wandering in response to food availability” (Forshaw & Cooper 1989), but I found reports of regular seasonal movement in the northern part of Central America and in Mexico. There are reports of Scarlet Macaws in Honduras moving seasonally to feed on pines (Portillo Reyes et al. 2004; Portillo Reyes et al. 2005a; Portillo Reyes et al. 2005b; Portillo Reyes 2010; Bonta, pers. comm. 2005). In Mexico, there is evidence of Scarlet Macaw seasonal food shifts and elevational migration (Rovirosa 1887; Binford 1989).

Radio-tagging eight Scarlet Macaws showed a seasonal migration of about 100 km from their breeding ground in the northern part of the Petén region of Guatemala to near Parque Nacional Sierra Lancandón where their diet changed due to different habitat (Rodas et al. 2001; Rodas 2002). Satellite-collaring allowed Bjork & McNab (2007) to study movement of Scarlet Macaws in the Petén of Guatemala for a few months at the end of the breeding season; the birds moved up to 25 km (Boyd & McNab 2008). Boyd & McNab (2008) conclude:

> Scarlet Macaw biology is very seasonal in the El Perú area (and the other monitored areas). The macaws are not year-round residents. Their presence in the monitored areas is presumably due to the food resources that become available in those locations during the macaw breeding season and because of the availability of nest sites.

In Central America I found one study, and a few observations, of Scarlet Macaw presence, diet, and food availability. Phenology work with Scarlet Macaw food trees was done in the Yaxchilán, Mexico, area, but a report merely mentioned this work and contained no phenology results (Rodas et al. 2001). At Maquenque, Costa Rica, most Scarlet Macaws were observed in black afara (*Terminalia ivorensis*) at the peak of its fruiting; teak (*Tectona grandis*) was fruiting when the Scarlet Macaw population spiked (Penard et al. 2008). The number of plant species eaten by captive-raised, reintroduced Scarlet Macaws in Costa Rica increased from 18 in the wet season to 27 in the dry season (Matuzak et al. 2008).

Seasonal Movement of Scarlet Macaws in Belize

Several authors have discussed the locations and movements of Scarlet Macaws in Belize (Russell 1964; Barlow & Caddick 1989; Kainer 1990), but Mallory (1991), in the Raspaculo Branch area, was much more successful in collecting sightings. Based on 22 days of observations in May at Cushta Bani (or Cuxta-Bani), a site in the upper reaches of the Raspaculo Branch near the crest of the Maya Mountains, Mallory (1994) showed a predominance of high overflights on an east/west axis and suggested that macaws might cross over the Maya Mountains to forage in the Cockscomb Basin. As a follow-up to this conjecture, a team trekked up the Raspaculo Branch valley in March and reported flights of macaws over the crest of the Maya Mountains flying in a south-southeast trajectory, possibly toward Red Bank Village – but in August no sightings were obtained from this location (Matola & Sho 2002a). Recorded notes on flight direction of Scarlet Macaws in the Las Cuevas Research Station area have been maintained since 1995 (Bol & King 1996; King 1998a), but were not analyzed. The belief of Red Bank villagers that macaws would consistently appear at Red Bank in the dry season when the polewood fruited led to the development of an ecotourism project focused on these birds (Romero 2004).

METHODS

STUDY AREA

The study area is approximately 5,199,000 km^2 and includes the Maya Mountains, as well as the sites of all known Scarlet Macaw observations after 1980 (Fig. 4). The Maya Mountains have great geographical variety and have been designated an Important Bird Area, one of six in Belize (Burke et al. 2009). Within this area are 16 major protected areas (Appendix C). Based on extensive literature research and personal observation I am reasonably certain that all current observations of wild Scarlet Macaws in Belize are contained within the study area.

Human habitation is minor in the interior of the study area and is limited to natural and cultural resource agency staff, Chalillo Dam facilities, Las Cuevas Research Station, and a few small tourist establishments. Nonetheless, human impact is notable because of previous or current logging activities, and the military exercises conducted by British, US, and Belizean forces. At the north-east and south edges of the study area are small Belizean villages; to the west, there are Guatemalan villages on the border. The only road access to the study area is via a seasonally maintained dirt road, best accessed from San Ignacio, which allows access to poorly maintained or abandoned logging roads which also serve as firebreaks. In the wet season all dirt roads can be very difficult to traverse or impassable, even with 4-wheel drive vehicles.

Vegetation in the study area is described in general terms as subtropical lowland broadleaf forest and shrublands in the lower-elevation areas east of the Maya Mountain crest; vegetation west of the crest is generally characterized as subtropical submontane broadleaf forest with submontane pine forest (Meerman & Sabido 2001). Climate in the study area is subtropical, with pronounced rainy and dry seasons and annual rainfall from 1,524 mm in the north, to 4,064 mm in the far southern part of the study area (National Meteorological Service 2006) or a minimum of 1,206 mm and maximum of 4,085 (Fig. 5) (Hijmans et al. 2005). Average monthly rainfall in Belize dramatically rises in May, peaks in July, steeply declines through October, and slowly moves to a low for the year in March. Dry season is mid-October to mid-May. For purposes of this paper, dry season will be considered to occur from November to April and wet season from May to October.

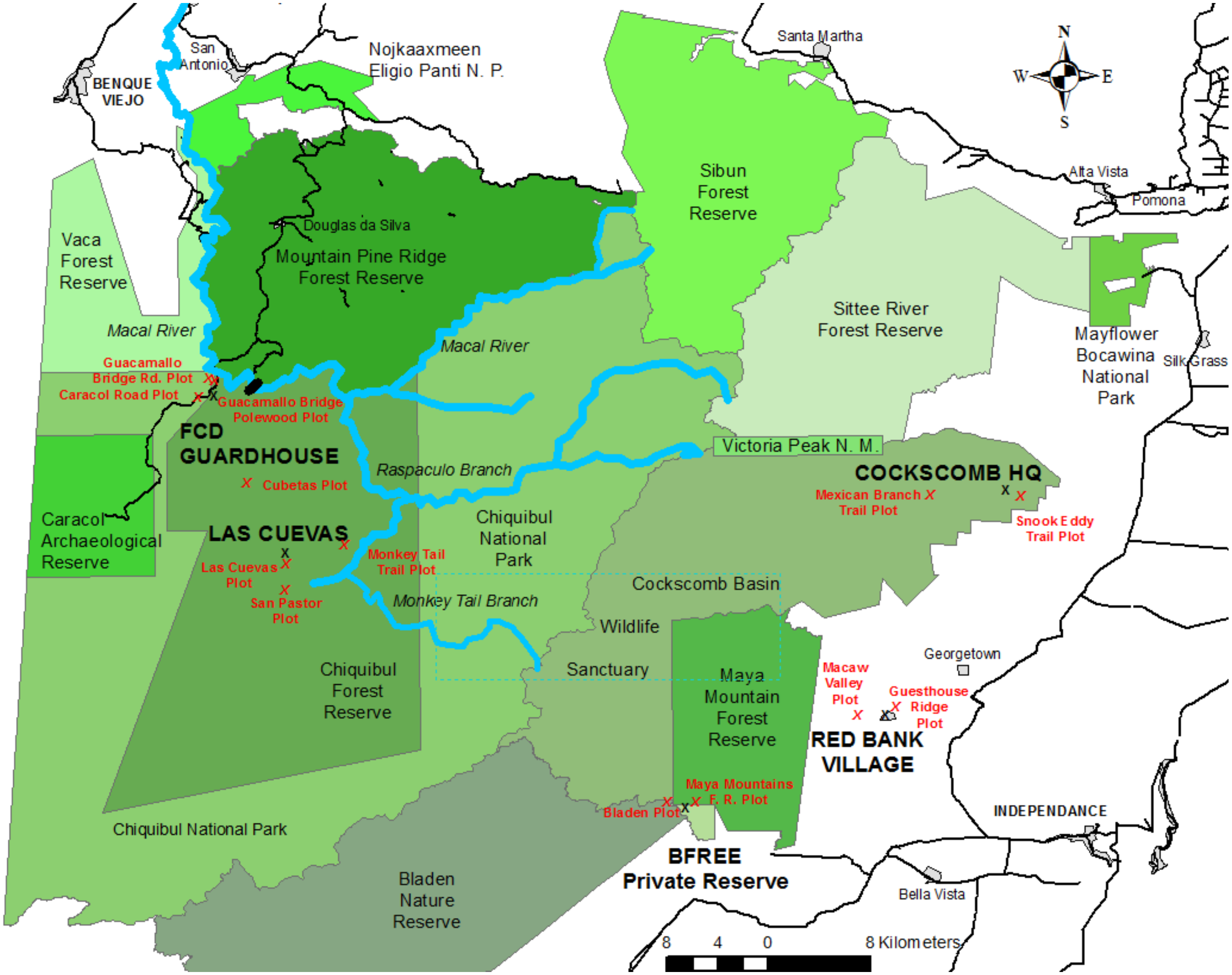


Figure 4 Study area map with protected areas, research plot locations, and other sites. Base map from Meerman & Sabido (2001).

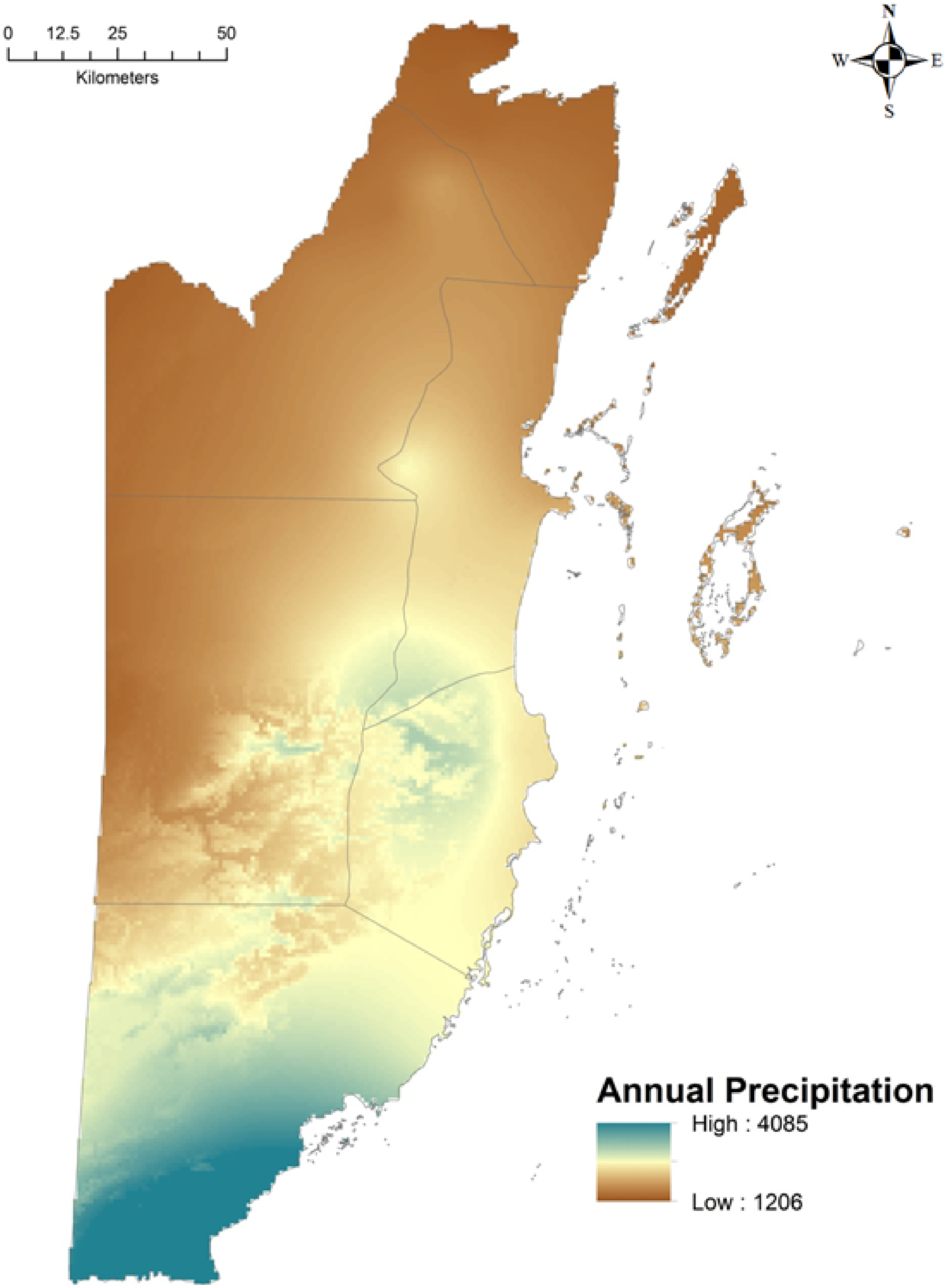


Figure 5. A summary of annual rainfall (mm) for Belize (1950-2000). Based on data provided by http://www.worldclim.org, using approach described by Hijmans et al. (2005).

There is a large difference in rainfall between the lower and eastern part of the study area, including the research areas of Cockscomb Wildlife Sanctuary, Red Bank Village, and the Belize Foundation for Research and Environmental Education (BFREE), and the western, higher and drier Chiquibul area, including the Las Cuevas Research Station and the FCD Guardhouse research sites. The meteorological station that best approximates the lower eastern research sites is at the Melinda Forest Station, where rainfall from April 1994 to May 1995 was 2,428 mm (Silver 1992). Although the data are only for one year, a pronounced downward trend in rainfall occurs in the months of November to April, the dry season, and this is typical of the area and the country. By comparison, annual rainfall is much less in the higher-elevation Chiquibul area, which includes the research sites of Las Cuevas and the FCD Guardhouse; the Chiquibul also has a pronounced dry season. Belize's National Meteorological Service records show that the annual rainfall in the Chiquibul area from 2001 to 2009 averaged 1,361 mm (Smith, pers. comm. 2010).

Temperature in the study area varies because of elevational differences and seasonal weather. Temperatures swings in the low-elevation areas of this study are moderated by proximity to the Caribbean to a greater extent than in the inland Chiquibul area. In addition, adiabatic temperature loss occurs in high-elevation areas, making one such site at 950 m an average of 4.8 °C cooler than at sea level (National Meteorological Service 2006). The combination of adiabatic cooling and less oceanic moderation makes the study area's high-elevation areas significantly cooler than low-elevation areas. If a graph is made of the number of days a northern cold front passes over Belize, then a steep bell curve appears, showing January as the coldest month throughout the country (Fig. 6).

The Chiquibul area is synonymous with the 177,000 ha Chiquibul Forest (Bridgewater et al. 2006a), which includes some savanna (Hicks et al. 2011), and is characterized by a mosaic of subtropical evergreen and seasonal forest, the result of variation in soil type and climate. The Maya Mountains ringing the Chiquibul to the east and south add a montane component with elevations up to 1,124 m at Doyle's Delight, Belize's tallest point (Teul 2009). Vegetation of the Chiquibul and Maya Mountain areas has been described on a broad scale (Wright et al. 1959; Iremonger & Brokaw 1996; Meerman & Sabido 2001; Penn et al. 2004; Bridgewater et al. 2006a). Vegetation has been described in detail at these high-elevation sites in the study area, all in the Chiquibul: Cuxta-Bani (or Cushta-Bani) on the Raspaculo branch of the Macal River (Brokaw 1991); Guacamallo Bridge on the Macal River (Urban et al. 2006); along the Macal River and Raspaculo branch of the Macal River (Minty 2001); at the San Pastor savanna in the Chiquibul (Hicks et al. 2011), and via numerous botanical studies at or near Las Cuevas Research Station.

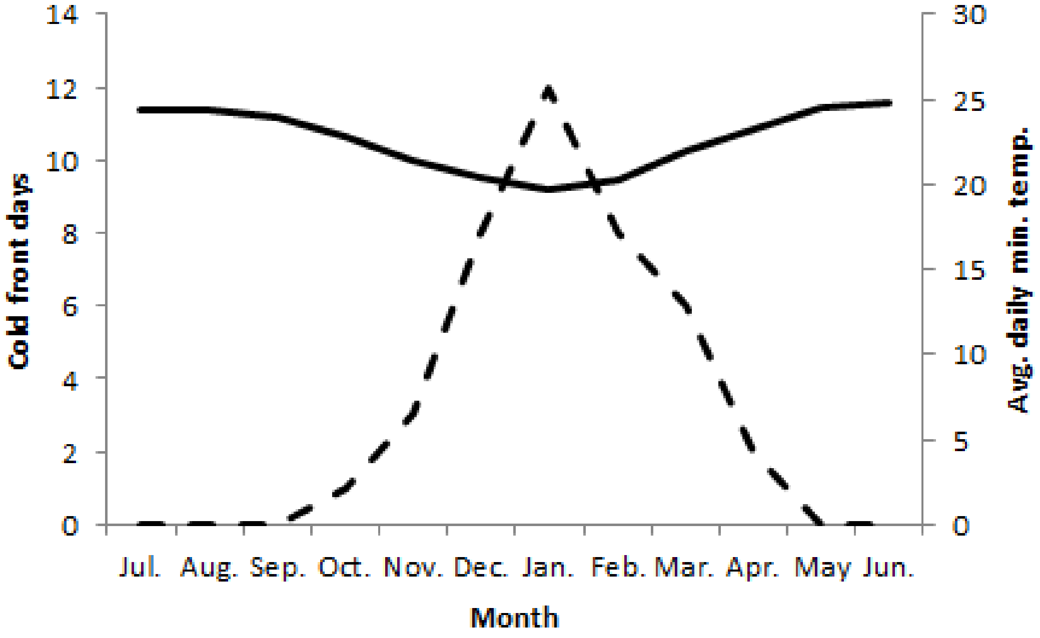


Figure 6. Cold fronts and average temperatures in Belize. Data from National Meteorological Service (2006). The dashed line is the number of days per month (1994-1998) that cold fronts impacted temperature. The unbroken line is monthly average daily minimum temperature from 32 years of data collected at Philip Goldson International Airport.

Vegetation was described in one key low-elevation research site in the study area: Red Bank Village (Meerman 1999, 2002); vegetation work was also done in the low-elevation Bladen area (Brokaw et al. 1987; Brewer & Webb 2002; Brewer et al. 2003), but not near my research sites at BFREE.

MACAW-FOOD PLANT ABUNDANCE AND PHENOLOGY

Phenology Plots

The only country-wide ecosystems map of Belize (Meerman & Sabido 2001) was used to identify sites for twelve phenology plots (2 m x 500 m). Strip plots to measure trees had been used in difficult terrain in southern Belize (Brewer & Webb 2002; Brewer et al. 2003) and I found this 500 m length compatible with linear transect-based bird point counts. Six of my plots represented “high” elevation ($\bar{x}$ =

535 m) areas west of the Maya Mountains crest in the Chiquibul area; another six plots represented “low” elevation ($\overline{x}$ = 94.67 m) areas east of the Maya Mountains crest in the foothills abutting the coastal plain. Phenology plots were located within known macaw habitat, as determined by previous sighting records, so that I could conduct point counts of macaws on them. Five of the low-elevation plots were in slight variations of lowland broad-leaved moist forest; the other plot was in shrubland surrounded by lowland broad-leaved moist forest. Four of the high-elevation plots were in submontane broad-leaved moist forest; the other two plots were at the upper boundary of lowland broad-leaved moist forest at 400 m. The phenology plots were constructed with a mix of paid and volunteer personnel from February 2009 to July 2009. My original goal of placing plots on contour to eliminate any elevation variation (Kaplin et al. 1998) was mostly met, but field conditions and available labor created some elevational variation within plots. Each plot had a randomly selected start point, and other plots were >1 km distant. Elevations of plots are compared below (Figs. 7, 8). Details of each plot are in Appendix D.

An additional *ad hoc* “plot” within the high-elevation Chiquibul area, the Guacamallo Bridge Road Polewood plot, length 291 m, was created as a line transect with no specific area along one edge of a road with abundant polewood, in order to compare phenology for polewood in the high-elevation Chiquibul area with polewood in the low-elevation Red Bank area. As I walked along the road edge I stopped every eleven steps, found the polewood tree closest to my position on that side of the road and noted fruit abundance and ripeness. The number of trees sampled varied, but was approximately 38.

Phenology Sampling

In phenological studies of avian diet, a common measurement of trees is at 130 cm from the ground, diameter at breast height (dbh). Measuring dbh is the most consistently accurate method of indirectly estimating fruit quantity (Chapman et al. 1992). Fruit quantity estimates based on the summed dbh of fruit-bearing trees were correlated with visual phenological transects, which also consistently produced accurate fruit quantity estimates (Chapman et al. 1994). Fruit abundance has been estimated through three data collection methods: fruit traps, a fruit trail where fruit on trees was visually scored, and phenological transects where fruit on trees was visually scored and the dbh measured. In a study comparing these methods, there was a high positive correlation between basal area and fruiting in the phenological transects, and positive correlation between volume of fruit found in fruit trails and in the phenological transects; fruit traps were not correlated to the other two methods, and were labor intensive (Chapman et al. 1994). Parrot researchers have used fruit trails and phenology transects to estimate seasonal abundance of fruit for several species of parrots (Ragusa-Netto 2005, 2006; Ragusa-Netto & Fecchio 2006; Ragusa-Netto 2007a, b, c). A combination of dbh and phenology transects has been used in diet studies with parrots (Renton 2001; de la Parra-Martinez & Renton 2010), and with primates (Basabose 2004). In each phenology plot, all Scarlet Macaw food trees known to occur in Belize and Guatemala, plus any unidentified trees, whether fruiting or not, were numbered by tag and had their dbh measured if the bole was ≥ 10 cm dbh, and the bole's center was within the plot. In multiple stemmed trees, the dbh of each stem was measured and summed as if they were one tree. Trees that were at a slant or parallel to the ground were measured at the point closest to the center line of the plot. Brewer et al. (2003) used a dbh measurement of ≥ 5 cm as a cut-off.

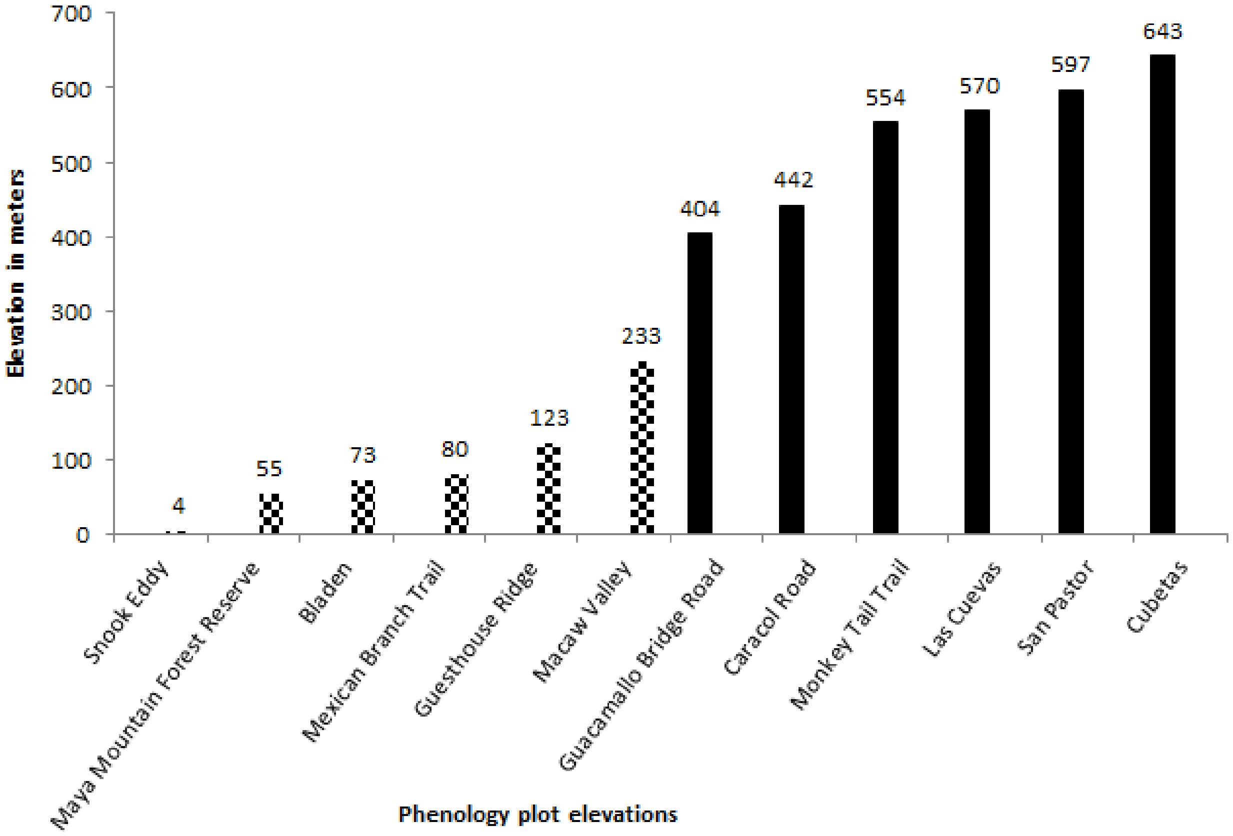


Figure 7. Elevation of phenology plots in Belize. Checkered bars represent phenology plots in lower-elevations found east of the Maya Mountain Crest in the foothills. Solid bars represent phenology plots in higher-elevations found west of the Maya Mountain Crest in the Chiquibul area.

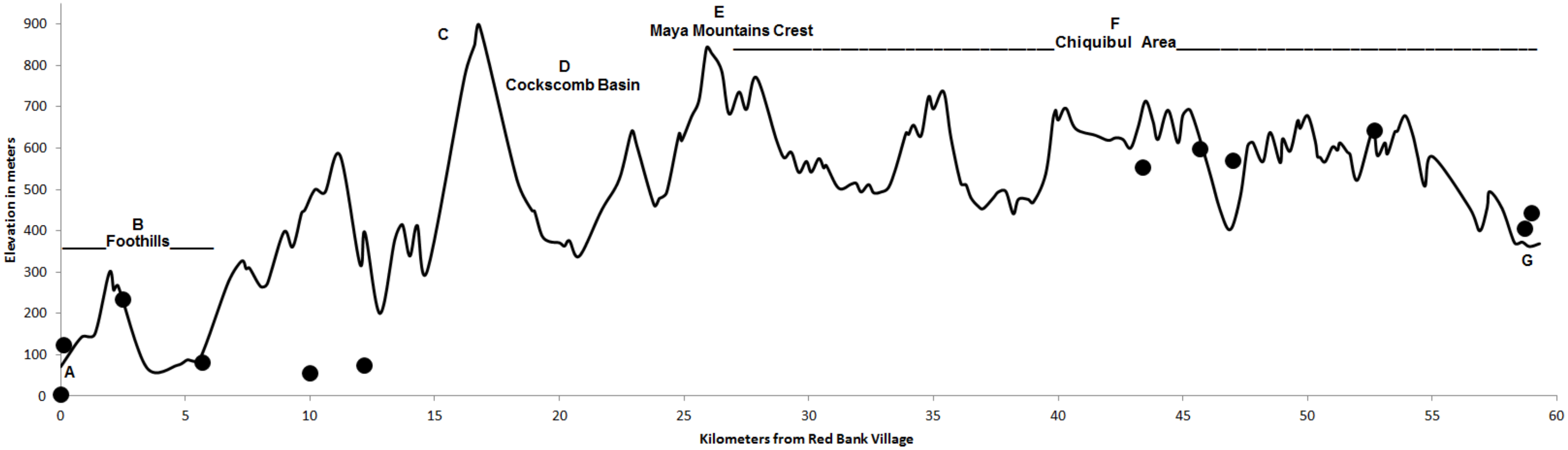


Figure 8: Topographic profile from Red Bank Village to Guacamallo Bridge, Belize, with plot locations. The line indicates approximate elevation along a straight-line path, data from Google Earth (2012). Circular points indicate plot elevation and distance from Red Bank Village along the profile line; no plots were directly on the profile line. A = Red Bank, B = low-elevation foothills, C = a high ridge along the profile, D = a valley within Cockscomb Basin, E = Maya Mountains Crest, F = the Chiquibul Area, G = Guacamallo Bridge on the Macal River.

point in vegetation plots in Belize, but I measured trees with dbh ≥ 10 cm because Scarlet Macaws tend to feed in large, canopy trees. In addition, Whittaker plot sampling (Comiskey et al. 1999) of known macaw-food trees at Red Bank during a pilot project in 2007, indicated that larger trees were more likely to have fruit.

Fruit and flowers may be hidden in the canopy, because of size, color, or line-of-sight obstruction by leaves and branches. Some researchers have sampled all fruiting trees to determine biomass, with no mention of how much crown could be seen, and fruit in hidden areas of the tree was estimated from other areas having fruit (Chapman et al. 1992). Another study estimated amount of fruit from all trees visible (Renton 2001), but no mention was made of visible tree crowns, and it seems likely visibility was not 100%. Ragusa-Netto (2006) initially did not specify how much tree crown was visible, but later sampled trees for the amount of fruit when 80% of the crown could be seen (Ragusa-Netto & Fecchio 2006; Ragusa-Netto 2007a, c). Striking a balance between not estimating fruit amounts in hidden areas and excluding trees that could be fruiting, I sampled for amounts of fruit in known macaw-food trees with at least 50% of the crown visible, and having a dbh ≥ 10 cm. Once started, sampling of eligible trees continued regardless of visibility changes brought on by seasonal changes in leaf density.

I kept no records of trees not meeting my methodology requirements, but to estimate numbers of trees excluded from sampling, I analyzed the Guacamallo Bridge Road plot because it had the greatest number of tagged trees (*N* =191) and greatest species diversity (*N* = 36). Aside from those trees not meeting the minimum dbh requirement, few trees were initially excluded from tagging and sampling, because identification was lacking in July 2008, the first month sampling occurred on this plot. In July 2008, 61 trees excluded – all due to insufficient canopy visibility; roughly half (*N* = 33) were macaw-food trees. The trees sampled (*N* = 158), included 97 macaw-food trees and 61 non-macaw-food trees, the latter sampled out of an abundance of caution. As identification progressed in all plots, non-macaw-food trees were dropped from measurement and analysis. Measurement of all trees on a plot is not necessary if a bird's food species are known (Blake et al. 1990); with the minor exception of Cohune Palm (*Attalea cohune*), none of the excluded species were discovered to be food species later.

Determining if a tree's fruit was botanically ripe (having mature seeds) was difficult because identification literature was lacking, the plots contained large numbers of tree species and individuals, and fruit was often too high for collection. Actually, fruit ripeness for macaws may be distinct from botanical ripeness because they often eat immature fruit. I assumed that fruit eaten by macaws was at their preferred ripeness, but I had very few feeding observations aside from wild annatto and polewood in the Red Bank area. Polewood, in abundance at Red Bank, was enthusiastically eaten by macaws when the aril was red or pink; the color may have indicated that the seeds were mature. I noted these fruit colors for polewood: brown (very immature), green (maturing), pink (more mature), and red (ripe). Not knowing botanical ripeness of the 103 species sampled, or the macaws' preferred ripeness for each species, I included fruit of any ripeness in fruit sampling records, which may have exaggerated fruit availability for macaws.

With few exceptions, each plot was sampled once within the last two weeks of each month from July 2008 through June 2009 (Appendix D). Tree fruit and flower abundance and phenology were observed on plots with binoculars. I estimated the amount of fruit and flowers in tree crowns by using a 0 to 4 abundance score so that 0 = 0% of branches had fruit, 1 = 1-25% of branches had fruit; 2 = 26-50%; 3 = 51-75%; and 4 = 76-100% (Chapman et al. 1994; Holbrook et al. 2002). I also noted presence or absence of flowers and fruit on the ground (Kaplin, pers. comm. 2009), and took photos and physical samples to identify plot trees. I photographed most tagged trees (leaves, any fruit or flowers, bark, and slash cuts in the bark), particularly unknown trees. Collection of fruit and leaves was done with a Snap-Cut® No. 11 Tree Trimmer Head, on up to five 6-foot long poles. Data were collected and organized into folders for each possible macaw-food species.

Physical samples and identification photos were shown to botanical experts; samples and photos were also compared with botanical literature, web- based herbarium photos, and herbarium specimens in Belize. Tree identification was provided by Dr. Stephen Brewer, tropical plant ecologist associated with the Belize Foundation for Research and Environmental Education (BFREE) (Brewer & Webb 2002; Brewer et al. 2003); he identified all trees in the Bladen and Maya Mountains Forest Reserve plots and gave identifications based on tree photos and physical samples from plots in Red Bank, Cockscomb, and sometimes from the Chiquibul area. Jan Meerman, field botanist and co-author of Belize's current vegetation map (Meerman & Sabido 2001) plus many other publications on Belize's plants and vegetation, provided tree identification based on tree photos and physical samples from the seven western Chiquibul plots, building on field identification by Nicodemas Bol from Las Cuevas Research Station (LCRS). Hector Mai, manager of the Forest Department Herbarium, identified a few specimens and allowed access to the herbarium, where I photographed known macaw-food species for comparative purposes. I used the Tropicos web site as the final authority on taxonomy (Tropicos.org 2010). The multiple languages of Belize made common names difficult to work with; modifiers such as “red,” “white,” “black,” “male,” or “female” were often ambiguous.

Following Holbrook et al. (2002), a monthly fruit availability index (FAI) was created for each species in the twelve phenology plots by using the following formula:

$$\mathrm{FAI} = \sum_{x=1}^{n} (\mathrm{bm}_x * \mathrm{pf}_x * \mathrm{ph}_x)$$

Biomass index (bm_X) represents the mean basal area per hectare for each species x and is determined by the dbh measurement of each qualified tree (≥ 10 cm dbh and ≥ 50% tree crown visible) in a 2 x 500 m plot. The proportion of fruiting individuals for species x is (pf_X), and (ph_X) is the average phenology score of all sampled individuals of species *x*. The average phenology score is a monthly average index of sampled estimates of tree crown fruit, converted to midpoint percentage values (i.e. 1 =1–25%, 2 = 26-51%) (Holbrook et al. 2002).

To extend this investigation beyond my own phenology plots, I collected macaw-feeding records from all literature on Scarlet Macaws in Belize; I also collected presence records for all known macaw-food trees in southern Belize (≤ 17.5° N latitude), noting locality and any phenological information (Appendix F). Unless the record specified otherwise, any mention of fruit or flower presence in the above records resulted in a conservative phenology score of 1 (1-25% presence in the tree). Records were added to my database even if they had been identified only to the genus level, something common in feeding observations.

MACAW OBSERVATION

Macaw Point Counts

Two general methods for sampling presence of parrots are “look up” and “look down” (Marsden 1999). “Look up” methods entail viewing from the ground, but closed tropical tree canopy along phenology plots hinders visual observations; if the parrot species is rare, this difficulty could result in few sightings in 12 months (*N* = 136, monthly avg. = 11.33) (Ragusa-Netto 2006). Using “look up” methodology in dry tropical forest, Renton (2001) walked trails near phenology plots during 19 months and had a similar number of observations (*N* = 207+, monthly avg. = 10.89+). My study area was largely composed of high canopy forest, and despite the Scarlet Macaw’s raucous call telling of its presence and general movement, it was often difficult to observe individuals directly from the ground. I conducted monthly ten-minute “look up” bird point counts at 0 m, 250 m, and 500 m within each plot, a sufficient distance apart to minimize double counting (Marsden 1999). These point counts were conducted in the morning and all were under tree canopy.

“Look down” methods entailing views from above the canopy are more appropriate for rugged terrain if access can be found or created (Marsden 1999). In addition to using ground-based observation, the Wildlife Conservation Society – Guatemala (WCS-Guatemala) also places observers in towers and emergent trees, and along cliffs (Garcia et al. 2004); well-positioned observers can sight Scarlet Macaws within a 2 km radius (Karubian et al. 2005). I set up two monthly “look down” point counts, one at low elevation and one at high-elevation with both sites within 1 km of a phenology plot. These point counts were most often conducted in the afternoon, after the morning plot point counts. The first site was accessed from the low-elevation Red Bank Village, Sho’s Fine Vista, and “looked down” and across Macaw Valley. This site was on a ridge and offered essentially a 180° view on one side; by moving to the other side of the ridge most of the other 180° could be observed. The second site was at Guacamallo Bridge on the Macal River and was intended to be representative of the high-elevation Chiquibul area. This site was equivalent to a “look down” because of its unobstructed 360° view.

Observation techniques differed somewhat for different two point counts but recording methods were the same for all point counts. I used binoculars for all point counts and added a 40-60x spotting scope for the two “look down” point counts at Red Bank and Guacamallo Bridge. I recorded the presence of all bird species on all point counts, whether seen or heard; any visual Scarlet Macaw sightings, of individuals or groups, were counted, not estimated. Because it is difficult to identify calls of individual birds, all aural records of Scarlet Macaws were conservative, likely resulting in lower numbers than reality. For example, if I heard macaw calls coming from two different places, the number of individuals was recorded as two, although there were likely more because macaws most often are in pairs.

I continued the practice of noting flight direction of macaw sightings (Bol & King 1996; King 1998a), and so was able to compare flight direction by month in the Las Cuevas area of the Chiquibul. Different feeding or flight behavior by the same macaw(s) was described as two or more records so that different behaviors could be analyzed. For example, if six macaws landed on a polewood and ate, then three flew to a wild annatto, this was recorded as two groups: one of six individuals, one of three. When a group of six pairs flew over Las Cuevas and landed, followed by one pair of the six heading east and the rest heading north, this was recorded as three records: one of twelve individuals, one of two, and one of ten. In determinations of high numbers of individuals for a day or month, great care was taken not to count individuals or groups of macaws twice, so in the examples above the census numbers would be six in the first example, and twelve in the second.

Determining abundance of feeding parrots, their food preferences, and seasonal consumption of food has been done by counting “feeding bouts.” A feeding bout is described as one observation of one or more parrots feeding on one food source; if the parrots fly to another food source during the period of observation, this is recorded as a second feeding bout (Galetti 1993; Renton 2001; Symes & Perrin 2003a; Ragusa-Netto 2006). Although I attempted to record all macaw feeding bouts, this was not possible at Red Bank because of the large numbers of macaws there. The opposite was true in the Chiquibul, where I rarely saw any macaws feed. I was able to record the seasonal diet of the macaws, but used direct observation to determine their abundance.

I added to my own Scarlet Macaw records, sightings from a compilation of published and unpublished literature, and from museums, web-published trip lists, list-serves, and personal communications (Appendix B). Published bird observations within the study area but not mentioning macaws were considered absence records. To this database I added other macaw observations transcribed by me from handwritten records in field station wildlife-observation logbooks or reports. Misidentification of macaws was not likely in these logbooks because of the unique size, coloration, and raucous call of macaws, and because most records came from people associated with the conservation field. Dates, times, and numbers of macaws described in observations by others were not always complete or exact, but still yielded important information.

Determining Macaw Abundance

Abundance of parrots may be estimated by maximum numbers seen during a specific observation time (Symes & Perrin 2003a; Berg & Angel 2006; Berg et al. 2007). An abundance index, if it is continually refined via periodic estimates over time, may reflect trends in macaw populations. Point count sightings enabled me to assess relative abundance at specific sites on a monthly basis.

Given an approximate fledge rate of 20%, macaw population abundance can also be estimated by counting pairs and family groups (Munn 1992; Gilardi & Munn 1998; Renton 1998b; Brightsmith 2007; Matuzak & Brightsmith 2007). Brightsmith (pers. comm. 2007) noted that in flight, group size and behavior assist in determining pairs, single birds, and family groups; juvenile macaws are easier to identify soon after fledging because they exhibit shorter tails, poor flight, and dark irises. I recorded pairs and groups of Scarlet Macaws, but this was more difficult in the Red Bank area where the macaws were often in large flocks, so pair and family groupings were not clear.

MACAW OBSERVATION ANALYSIS

I had two sets of macaw sighting data to analyze. The first included only my own Scarlet Macaw sightings from point counts on my phenology plots, two other point counts (Sho's Fine Vista and Guacamallo Bridge), and some opportunistic sightings. My point counts were timed and conducted on a schedule, so I could determine the frequency of sightings. More point counts would have created a larger sampling of macaw presence through the months, but were not possible because of logistics. My presence was only occasionally noted by macaws.

A second set of data came from sightings by others, including historical sightings, yielding a larger pattern filling in months and years in which I had no sightings. Most sightings by others were not regular, nor systematic, nor timed, as my sighting data were. Yet that large number of sightings over many years should not be dismissed. As an indication of reliability, when graphed, the data of others and my data agree on general temporal and spatial trends.

I was aware that observer bias could impact data collected by others. A seasonal difference in the number of observers was dismissed by Las Cuevas staff. There is a substantial seasonal difference in observers at Red Bank Village because many more people come to Red Bank to see macaws in February and March than in July. This is not observer bias because no one except me visited Red Bank in July when no macaws were expected or seen. Observer bias could impact numbers of sightings because casual observers (eco-tourists) are more likely to come to Red Bank at the peak of the season. That could diminish the apparent relative use of the area by macaws before or after that peak.

Monthly graphs of abundance were compiled from both sets of sighting data to detect seasonal trends. I derived minimum population numbers from my point counts in which individual macaws were not recounted and from the simultaneous sightings of macaws by others in disparate localities. Using all sources I created maps to determine current and historical distribution, and evaluate any seasonal movement patterns that appeared.

RESULTS

MACAW DISTRIBUTION AND DIET

Macaw Distribution

My work had a wider scope than previous studies because it covered both low- and high-elevation areas, and my study covered an entire year. I added many macaw sighting records for the Toledo and Stann Creek districts and mapped all known Scarlet Macaw sightings in Belize (Fig. 9). Sinuous patterns of sightings and clusters emerged along roads and rivers. Sightings along roads and rivers appear to be due to ease of access; unlike roads however, the macaws use rivers as thoroughfares and often nest within them.

East of the Maya Mountain Divide a large cluster of sightings occurs at the Belize Foundation for Research and Education and at the nearby Bladen Nature Reserve where the Bladen River exits the foothills. The Bladen River valley upstream has macaw-food trees (Iremonger et al. 1995; Brewer & Webb 2002; Brewer et al. 2003), but extensive research in the area has yielded no sightings of this highly conspicuous bird (Brokaw et al. 1987; Marlin, pers. comm. 2009; Brewer, pers. comm. 2010). Macaw sightings have been reported north from the Bladen River along the foothills at Mattenson Camp and Trio, in the Toledo District (Mallory & Matola 2002b; Anon., pers. comm. 2009); at Red Bank and San Pablo (Meerman 1999; McRae 2000; Meerman 2002; Romero 2004; pers. obs. 2007-2009); at Maya Mopan (Anon., pers. comm. 2009); in the Cockscomb Basin (Kamstra 1987, 1996), and at Maya Centre and San Ramon (Anon., pers. comm. 2009). The most northern sightings in the Maya Mountain foothills have occurred at Mayflower-Bocawina National Park (Meerman et al. 2003; Bemer, pers. comm. 2007).

West of the Maya Mountain Divide, within the Chiquibul, there are sighting records from as far south as the Ceibo Chico drill site and Smokey Branch areas (Colston 1995), and sightings and nests along the Chiquibul River (Colston 1995; Britt 2010d). Macaws were not found on the southern side of the Maya Mountain Divide in the Columbia Forest Reserve (Parker et al. 1993; Meerman & Matola 1997), and have not been seen at Doyle’s Delight on the southeast crest of the Maya Mountains despite three expeditions (Teul 2009). To the far west, macaws are rarely found in Caracol, but were seen flying west across the border, presumably to Poptun, Guatemala (Bol, pers. comm. 2005). Mallory & Matola (2002b)

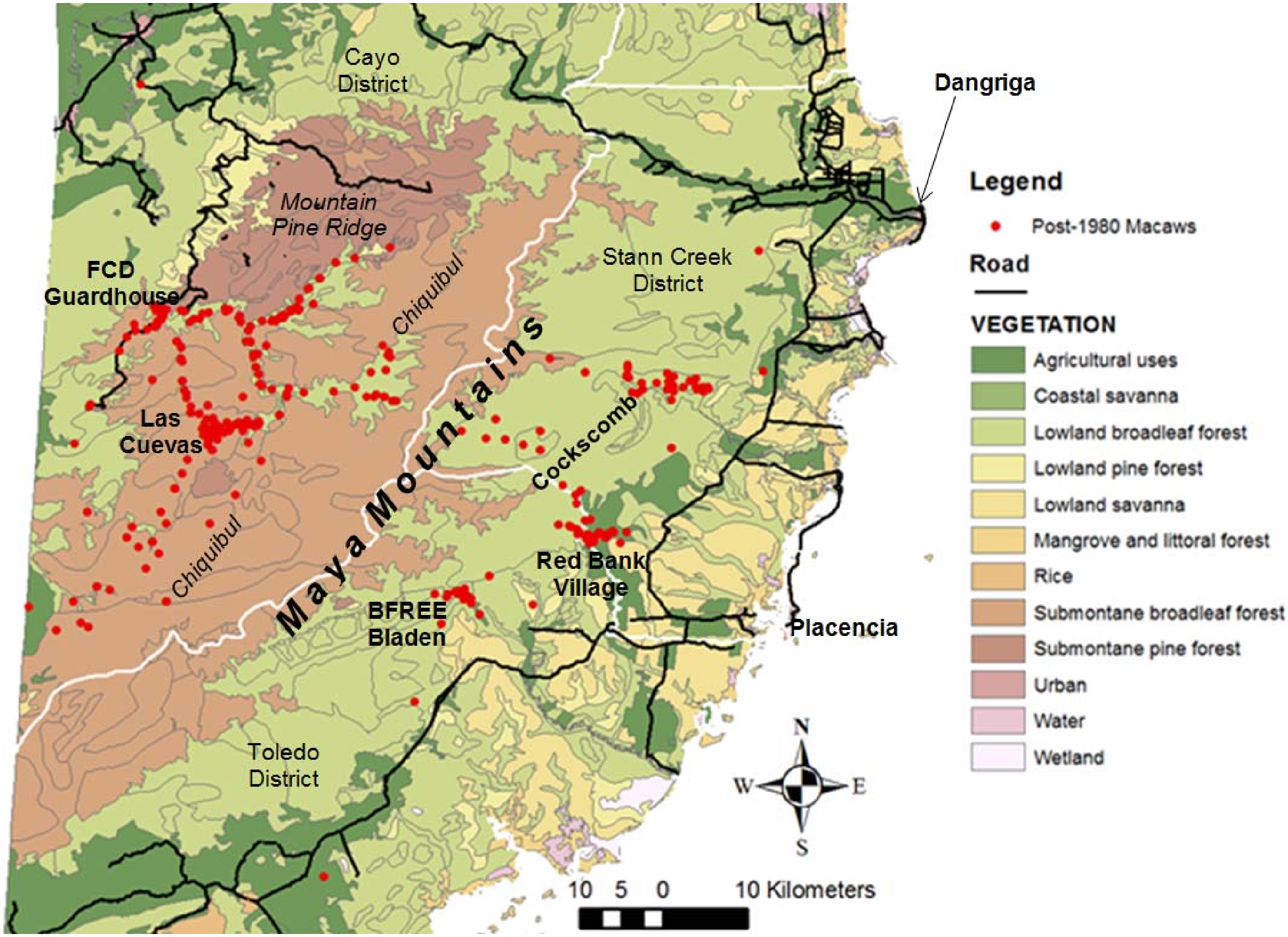


Figure 9. <u>Distribution of Scarlet Macaw records in Belize post-1980</u>. Points refer to unique location records (*N* = 1667) with varying numbers of Scarlet Macaws. See Appendix B for sources of Scarlet Macaw records not my own. Vegetation map by Meerman & Sabido (2001).

cite a personal source who saw macaws "flying west into Guatemala in the evening hours [likely late afternoon in American English] and eastwards into Belize." Villeda (2001) cites Perez (1998), whose work I have not been able to access, as reporting "low numbers in the pine forests of Poptun," about 23 km from the Belize border.

The Macal River appears to be the northernmost area where Scarlet Macaws can be found in Belize; Forest Department rangers at Augustine, in the heart of Mountain Pine Ridge, said in 1990 that the species had not been seen there for at least five years (Kainer 1990). Some macaws wander into the Mountain Pine Ridge near the Macal (Martinez, pers. comm. 2010), and one tagged macaw may have made it to the middle of the Mountain Pine Ridge while foraging (Britt et al. 2011).

The distribution of Scarlet Macaws in Belize is largely within 16 major protected areas (Appendix C). The most important protected areas are the Chiquibul Forest Reserve, Chiquibul National Park, and Cockscomb Wildlife Sanctuary; the important Red Bank area is unprotected government land. Sightings have been reported in the foothills (a mixture of unprotected government and private lands) to the north of Red Bank and up to Cockscomb, and to the south toward Bladen.

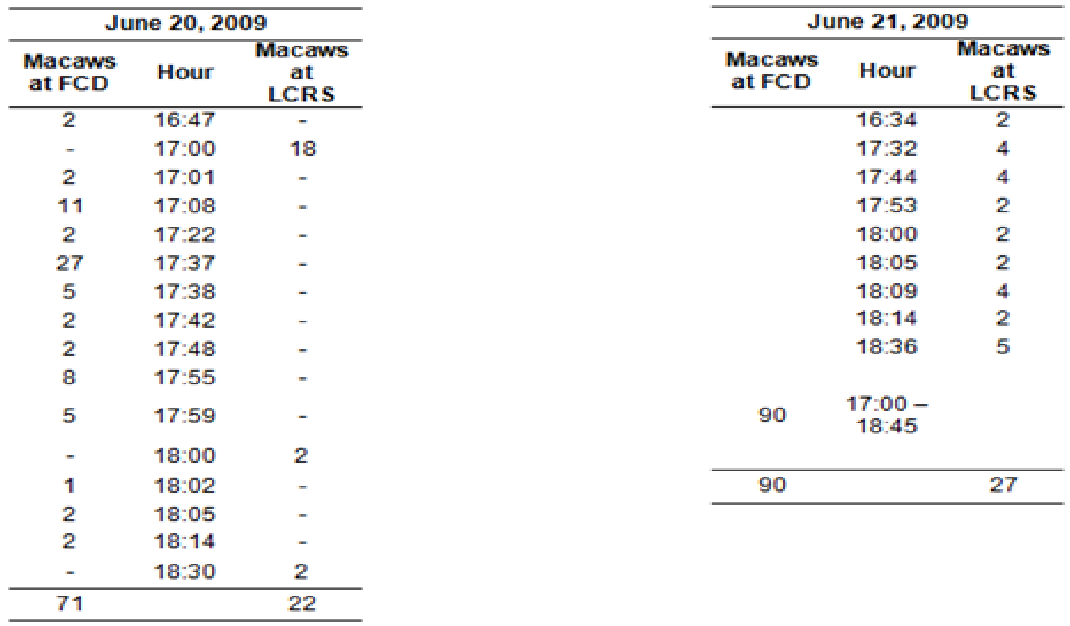
On three occasions I observed very large flocks possibly containing most of the macaws currently living in Belize. On February 19, 2008, while conducting a point count from Sho's Fine Vista in Red Bank, I counted 93 macaws as they flew in small groups over a ridge and out of Macaw Valley; that normal late-afternoon behavior probably represented movement to a roosting site at Sapote Creek off the Swasey River. Approximately 20 minutes later at the base of Sho's Fine Vista Trail, at the campground along the Swasey, I encountered another group of 23 macaws flying down the Swasey, for a total of 116 macaws for the afternoon. Those 23 macaws could have been from the group of 93 counted earlier, but the 93 were headed toward Sapote Creek, upstream, and the 23 were flying downstream. Since this observation occurred in February, and breeding in the Chiquibul is from January to July, it is likely that it did not include breeding individuals in the Chiquibul – some of which were surely on nests incubating eggs.

On June 19-21, 2009, very large numbers of macaws were seen at the Friends for Conservation and Development (FCD) Guardhouse at the Caracol Junction in the Chiquibul. At this location on June 20th between 16:00 and 18:14 I counted 71 individual Scarlet Macaws flying southwest to northeast toward the Macal River, approximately 1.7 km away (Table 3). They likely traveled upstream to roost sites along the river; this was their general movement pattern in the late afternoon, as shown by my Guacamallo Bridge point counts and the observations of others. During the same time period Celia Bol at Las Cuevas noted 22 individuals flying toward the east. Las Cuevas is a straight-line distance of approximately 14 km to the southeast from the FCD Guardhouse. Although Celia Bol’s sighting times are approximate, I believe her numbers are accurate since she has years of experience of hearing and counting Scarlet Macaws at Las Cuevas and logging them into the Las Cuevas Wildlife Sightings Book.

On June 21, 2009, FCD Rangers observed 90 macaws from the FCD Guardhouse flying southwest to northeast; almost simultaneously I observed 27 macaws at Las Cuevas flying west to east, giving a total of 117 macaws seen (Table 3). With the similarity of timing of sightings, dissimilar directions of flight, distance between observers, and observation sites not sharing a river traveling route in common, it seems highly likely that the birds counted at the FCD Guardhouse and Las Cuevas on those two days were not being counted twice.

Since it seems highly likely that there were macaws in other locations, the minimum population for Belize (during mid-June) must be greater than 117. I believe the large flocks seen on June 21, 2009, represent a majority of the nation’s macaw population, which I estimate not to exceed 200 individuals.

Table 3. Large Flocks of Scarlet Macaws at the FCD Guardhouse and Las Cuevas June 20, 21, 2009, Belize.



June 20, 2009		
Macaws at FCD	Hour	Macaws at LCRS
2	16:47	-
-	17:00	18
2	17:01	-
11	17:08	-
2	17:22	-
27	17:37	-
5	17:38	-
2	17:42	-
2	17:48	-
8	17:55	-
5	17:59	-
-	18:00	2
1	18:02	-
2	18:05	-
2	18:14	-
-	18:30	2
71		22

June 21, 2009		
Macaws at FCD	Hour	Macaws at LCRS
	16:34	2
	17:32	4
	17:44	4
	17:53	2
	18:00	2
	18:05	2
	18:09	4
	18:14	2
	18:36	5
90	17:00 – 18:45	
90		27

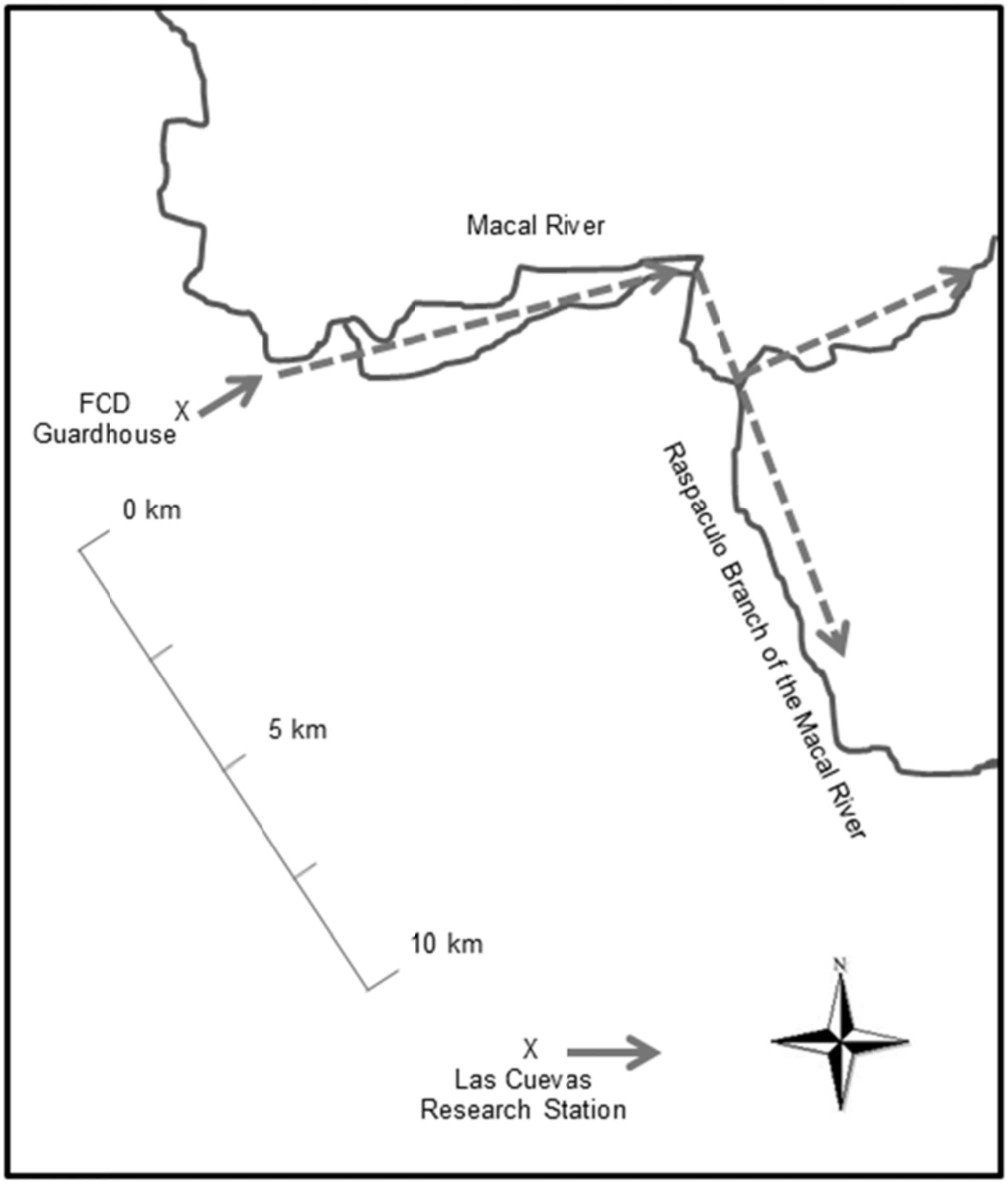


Figure 10: Riverine flight patterns in the Chiquibul area of Belize, June 21, 2009. Solid line arrows represent observed flight direction; dashed line arrows represent presumed flight directions.

Macaw Diet

Before this study only 25 food plant species for macaws had been reported in Belize. In Guatemala 35 food plant species had been reported (Villeda 2001; Moya & Castillo Villeda 2002), and in my visits to the Petén region of Guatemala I was told of additional food plants. Because the vegetation in the Petén area is similar to that of Belize (Miller, pers. comm. 2004; pers. obs. 2004), I expected the number of food plant species for Scarlet Macaws in Belize to be similar to those in Guatemala and, as expected, I found that to be true. I corrected typographical errors and updated taxonomy of all past

Scarlet Macaw feeding records, and combined them with my observations and interviews, producing a Scarlet Macaw food plant list for Belize of at least 70 species in 31 families (Table 4). Comparing diet in other Central American countries I found 31 plants in the macaw's diet unique to Belize. During this study, three species were identified as new food plants: the fruit/seed of the mo tree (*Pera arborea*) (pers. obs. 2009), leaflets of yemeri (*Vochysia hondurensis*) (pers. obs. 2009), and the nut of an oak (*Quercus* sp.) (Britt 2010b). Looking at all records from all sources, I found only one feeding record in each of the wet season months of June, July, August, and September, and no records from October, November or December.

Seasonality of Scarlet Macaw Food Plants in Belize

Fruit Availability in Phenology Plots

My phenology plots had 809 tagged trees from 40 families, including 97 genera and 103 species. Of 10,166 tagged tree sampling records, 9,157 (90.07%) were of trees identified as to species. Numbers of macaw-food trees per plot varied; the Guacamallo Bridge Road plot had several times the number of food trees and twice the number of individual species as other plots. Historic logging disturbance and proximity to a river might explain the high species richness on this plot, although less species-rich plots had similar site history and proximity to water. Tagged tree species are listed (Appendix E).

I calculated a Food Availability Index (FAI) score (Holbrook et al. 2002) and created monthly FAI graphs for the 12 plots (Appendix H) to show production of known macaw-food tees. The Guacamallo Bridge Road Polewood plot was the 13th plot and unique; it was focused on polewood phenology with no dbh measurements, and thus no volume or FAI score. Monthly FAI scores for low-elevation plots (Table 5) showed very high scores for wild annatto at Red Bank in May (FAI = 1079) and June (FAI = 964), which was 58.72% of the total annual FAI score for all low-elevation plots for that year; there were no Scarlet Macaws at Red Bank during those two months. Wild annatto at Red Bank had fruit, in varying stages of ripeness, during all months. The next highest annual low-elevation FAI scores were *Cecropia peltata* (763) and *Protium confusum* (702), congeners with *C. obtusifolia* and copal (*P. copal*) which have feeding records. Concentrations of polewood (annual FAI = 401) occurred December through March – the same time Scarlet Macaws were in the low-elevation areas.

Fruit availability index scores of three species in high-elevation plots, copal (943), nargusta (765), and red gumbo limbo (625), were two or three times higher than other species (Table 6). Fruit availability was not uniform in the high-elevation plots which had a very high peak in May (FAI = 1438) dominated by nargusta (FAI = 732) and poisonwood (*Pleradenophora longicuspis*) (FAI = 241). Low FAI scores were in July (67), August (53), and October (51). Despite September's FAI score of 157, July to October was a time period with much less fruit than the rest of the year. Red gumbo limbo (*Bursera simaruba*) had fruit year-round except in April; copal fruit was available for nine months. Wild cherry (*Pseudolmedia spuria*) fruit was present February to April and chicle (*Manilkara zapota*) from April through June.

Polewood in plots showed a marked seasonality depending on elevation (Fig. 11). Low-elevation plots had some ripe polewood starting in December with a peak in March, a time period when macaws were present, followed by no ripe polewood in April and no macaws until November or December.

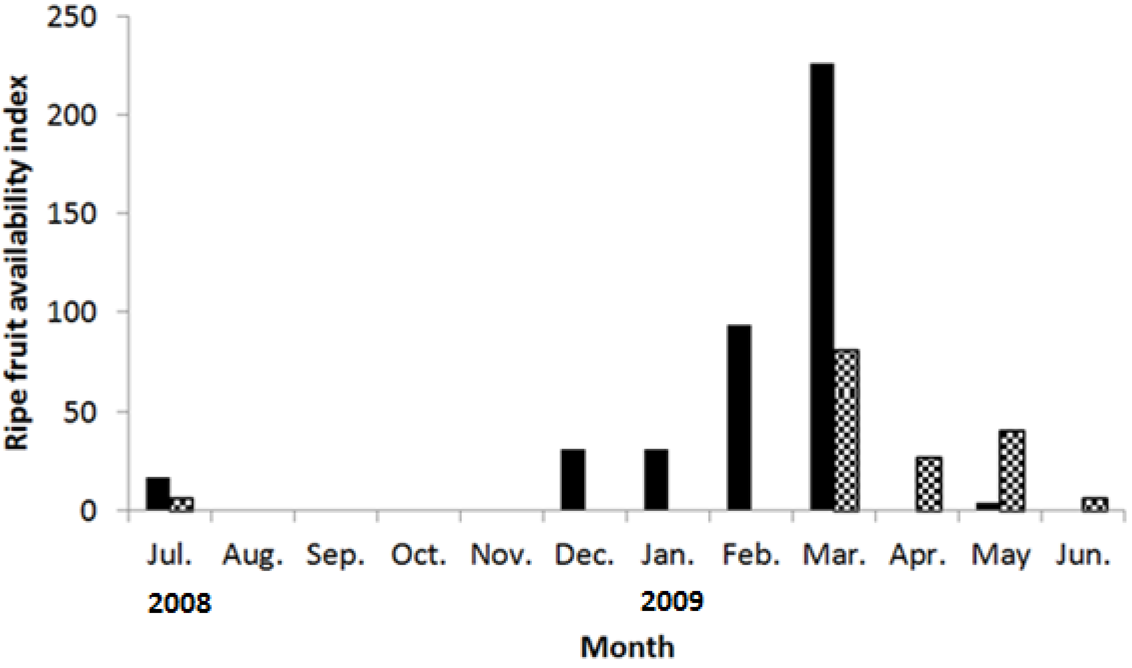


Figure 11. Ripe polewood (*Xylopia frutescens*) fruit availability index scores in low-elevation plots in Stann Creek and Toledo Districts, and high-elevation plots in Cayo District, Belize, from July 2008 to June 2009. Dark bars are low plots (*N* = 13 ripe fruit records); checked bars are high plots (*N* = 12 ripe fruit records).

Table 4. Scarlet Macaw food plant list for Belize.

Family	Genus	Specific Epithet	Plant Part Eaten	Source
Fabaceae	*Acacia*	sp.	Seed	Bol (pers. comm. 2009)
Apocynaceae	*Allamanda*	sp. [I suspect *cathartica*]	Unripe seed	Mallory & Matola (2002b)
Annonaceae	*Annona*	*reticulata*	Fruit/seed	Howe in (Bol & King 1996) and King (1998a, b)
Apocynaceae	*Aspidosperma*	*spruceanum*	Unknown	Bol (pers. comm. 2009)
Anacardiaceae	*Astronium*	*graveolens*	Unknown	Bol & King (1996); King (1998a, b)
Arecaceae	*Attalea*	*cohune*	Seed	Matola & Sho (1998); Renton (1998b); Minty (2001); Mallory & Matola (2002b); M^{c}Reynolds (pers. obs. 2007-2007)
Bombacaceae	*Bernoullia*	*flammea*	Flowers	Sho (pers. comm. 2010)
Moraceae	*Brosimum*	*alicastrum*	Seed	Minty (2001)
Burseraceae	*Bursera*	*simaruba*	Fruit/seed	Renton (1998b); Minty (2001); Mallory & Matola (2002b); Matola & Sho (2002a) and Sho (pers. comm. 2006)
Malpighiaceae	*Byrsonima*	*crassifolia*	Fruit	Kainer (1990)
Sterculiaceae	*Byttneria*	*catalpifolia*	Seed	Mallory (1991); Minty (2001)
Clusiaceae	*Calophyllum*	*brasiliense*	Fruit/seed	Kainer (1990); Bol & King (1996); King (1998a, b)
Moraceae	*Castilla*	*elastica*	Unknown	Bol (pers. comm. 2009)
Cecropiaceae	*Cecropia*	*obtusifolia*	"Fruit"	Renton (1998a); Minty (2001); Mallory & Matola (2002b)
Meliaceae	*Cedrela*	*odorata*	Unripe seed	Minty (2001); Mallory & Matola (2002b)
Bombacaceae	*Ceiba*	*pentandra*	Unripe pods, young leaves, flowers	Kainer (1990); Minty (2001)
Cucurbitaceae	*Cionosicys*	sp.	Unripe seed	Mallory & Matola (2002b)
Euphorbiaceae	*Cnidoscolus*	sp.	Unripe seed	Renton (1998b); Minty (2001)
Polygonaceae	*Coccoloba*	*belizensis*	Unknown	Bol & King (1996); King (1998a, b)
Fabaceae	*Cojoba*	*arborea*	Seed	Bol & King (1996); King (1998a, b)
Combretaceae	*Combretum*	*fruticosum*	Flower	M^{c}Reynolds (pers. obs. 2007-2009)
Combretaceae	*Combretum*		Flower	Mallory & Matola (2002b)
Boraginaceae	*Cordia*	*alliodora*	Unknown	Bol (pers. comm. 2009)

Family	Genus	Specific Epithet	Plant Part Eaten	Source
Annonaceae	*Cymbopetalum*	*mayanum*	Fruit/seed	Coc (pers. comm. 2007)
Fabaceae	*Dalbergia*	*stevensonii*	Unknown	Codd (pers. comm. 2009)
Araliaceae	*Dendropanax*	*arboreus*	Fruit/seed	Bol (pers. comm. 2009)
Fabaceae	Dialium	guianense	Seed (unripe)	Mallory & Matola (2002b)
Moraceae	*Ficus*	*glabrata*	Fruit/seed	Mallory & Matola (2002b)
Moraceae	*Ficus*	sp.	Fruit/seed	Minty (2001)
Sterculiaceae	*Guazuma*	*ulmifolia*	Seed	Renton (1998b); Mallory & Matola (2002b)
Fabaceae	*Inga*	sp.	Seed	Mallory & Matola (2002b)
Fabaceae	*Inga*	*vera spuria*	Seed	Mallory & Matola (2002b)
Chrysobalanaceae	*Licania*	*platypus*	Fruit/seed	Winston (pers. comm. 2010)
Lauraceae	*Licaria*	*peckii*	Unknown	Bol (pers. comm. 2009)
Tiliaceae	*Luehea*	*seemannii*	Unknown	Brewer (pers. comm. 2009)
Tiliaceae	*Luehea*	*speciosa*	Flower pod	Phillips (pers. comm. 2009)
Sapotaceae	*Manilkara*	*zapota*	Seed/fruit	Bol (pers. comm. 2009)
Lauraceae	*Nectandra*	sp.	Unknown	Bol (pers. comm. 2009)
Fabaceae	*Ormosia*	*velutina*	Unknown	Brewer (pers. comm. 2009)
Euphorbiaceae	*Pera*	*arborea* originally *barbellata* (Meerman)	Unripe seed	Meerman (1999); M^{c}Reynolds (pers. obs. 2007-2009)
Myrtaceae	*Pimenta*	*dioica*	Seed/fruit	Bol & King (1996); King (1998a, b)
Fabaceae	*Platymiscium*	*dimorphandrum*	Fruit/seed	BFREE Wildlife Logbook
Euphorbiaceae	*Pleradenophora*	*longicuspis*	Seed	Bol & King (1996); King (1998a, b); Renton (1998b)
Cecropiaceae	*Pourouma*	*bicolor*	Fruit/seed	Renton (1998b); Meerman (1999); Mallory & Matola (2002b)
Sapotaceae	*Pouteria*	*amygdalina*	Seed/fruit	Bol & King (1996); King (1998a, b)
Sapotaceae	*Pouteria*	*campechiana*	Undescribed	Bol & King (1996); King (1998a, b)
Sapotaceae	*Pouteria*	*sapota*	Seed/fruit	Bol (pers. comm. 2009)
Burseraceae	*Protium*	*copal*	Seed	Howe in (Bol & King 1996); King (1998a)
Moraceae	*Pseudolmedia*	*spuria*	Seed	Bol & King (1996); King (1998a, b)
Moraceae	*Pseudolmedia*	*spuria*	Seed	Bol & King (1996); King (1998a, b)
Burseraceae	*Protium*	*copal*	Seed	Howe in (Bol & King 1996); King (1998a)
Fabaceae	*Pterocarpus*	*officinalis*	Seed	Mallory & Matola (2002b)

Family	Genus	Specific Epithet	Plant Part Eaten	Source
Fabaceae	*Pterocarpus*	*rohrii*	Seed	Mallory & Matola (2002b); Las Cuevas Logbook (2009)
Fagaceae	*Quercus*	sp.	Nut	Britt (2010b)
Arecaceae	*Sabal*	*mauritiiformis*	Seed/fruit	Bol (pers. comm. 2009)
Araliaceae	*Schefflera*	*morototoni*	Fruit/seed	Meerman (1999)
Fabaceae	*Schizolobium*	*parahyba*	Seed	Renton (1998b); Sho (pers. comm. 2006)
Sapotaceae	*Sideroxylon*	*stevensonii*	Unknown	King (1998a, b); Bol (pers. comm. 2009)
Simaroubaceae	*Simarouba*	*glauca*	Fruit/seed	Pop (pers. comm. 2009)
Elaeocarpaceae	*Sloanea*	*tuerckheimii*	Seed	Mallory & Matola (2002b); M^c^Reynolds (pers. obs. 2007-2009)
Anacardiaceae	*Spondias*	*mombin*	Seed	Mallory & Matola (2002b)
Anacardiaceae	*Spondias*	sp.	Fruit/seed	Las Cuevas Log Book (2009), FCD Rangers (pers. comm. 2009)
Apocynaceae	*Stemmadenia*	*donnell-smithii*	Fruit/seed	Bol (pers. comm. 2009)
Fabaceae	*Swartzia*	sp.	Seed	Mallory & Matola (2002b)
Meliaceae	*Swietenia*	*macrophylla*	Unknown	Bol (pers. comm. 2009)
Combretaceae	*Terminalia*	*amazonia*	Fruit/seed	Bol (pers. comm. 2009)
Moraceae	*Trophis*	*racemosa*	Fruit/seed	King (1998a, b); Bol (pers. comm. 2009)
Bromeliaceae	Unknown		Stems, leaf bases	Renton (1998b)
Fabaceae	*Vatairea*	*lundellii*	Unknown	BFREE Wildlife Logbook
Myristicaceae	*Virola*	*koschnyi*	Seed	Salam (pers. comm. 2009)
Lamiaceae	*Vitex*	*gaumeri*	Seed	Mallory & Matola (2002b)
Vochysiaceae	*Vochysia*	*hondurensis*	Leaflets	M^c^Reynolds (pers. obs. 2007-2009)
Annonaceae	*Xylopia*	*frutescens*	Seed	Renton (1998b); Meerman (1999); Mallory & Matola (2002b); Matola & Sho (2002a); M^c^Reynolds (pers. obs. 2007-2009)
Rutaceae	*Zanthoxylum*	*belizense*	Unknown	Minty (2001)
Rutaceae	*Zanthoxylum*	*ekmanii*	Seed	Brewer (pers. comm. 2009)
Rutaceae	*Zanthoxylum*	sp.	Seed (unripe)	Mallory & Matola (2002b); Sho (pers. comm. 2006)

Table 5. Fruit availability index scores by species for low-elevation plots in Belize, July 2008-June 2009.

Food Plant	**Jul 08**	**Aug 08**	**Sep 08**	**Oct 08**	**Nov 08**	**Dec 08**	**Jan 09**	**Feb 09**	**Mar 09**	**Apr 09**	**May 09**	**Jun 09**	**FAI**
Annona reticulata (*N* =1)	3.9	7.9	-	-	-	-	-	-	-	-	-	2.0	13.7
Cecropia obtusifolia (*N*=1)	-	-	-	-	-	-	-	-	4.3	-	-	-	4.3
Cecropia peltata (*N*=16)	-	162.4	-	97.8	78.2	39.1	19.6	-	-	-	182.2	184.0	763.3
Cojoba arborea (*N*=1)	12.7	12.7	-	-	-	-	-	-	-	-	-	-	25.3
Cordia bicolor (*N*=1)	-	-	-	4.6	-	-	-	-	-	-	-	-	4.6
Dialium guianense (*N*=4)	-	-	-	-	4.7	-	-	-	-	-	-	2.0	6.7
Inga sapindoides (*N*=1)	-	11.9	-	-	-	-	-	-	-	-	-	-	11.9
Pourouma bicolor (*N*=1)	-	-	-	-	-	-	-	12.2	16.3	16.3	8.1	-	52.9
Pouteria durlandi (N=4)	-	-	-	-	-	-	-	-	-	-	11.1	-	11.1
Protium confusum (*N*=34)	-	12.4	-	35.8	38.4	53.7	157.6	73.6	139.2	64.3	76.0	51.3	702.5
Schefflera morototoni (*N*=3)	-	-	-	-	-	23.3	13.3	28.4	33.4	18.3	-	-	116.7
Sloanea tuerckheimii (*N*=31)	93.2	8.5	31.1	77.6	286.3	208.6	226.3	201.9	159.7	20.0	1079.3	964.6	3357.1
Spondias radlkoferi (N=2)	-	-	-	4.9	-	-	-	-	-	-	4.9	-	9.9
Stemmadenia donnell-smithii (N=4)	-	-	-	4.4	4.4	4.4	-	8.7	4.4	13.1	4.4	4.4	48.0
Trophis racemosa (*N*=6)	-	-	-	-	-	-	5.7	-	-	-	17.0	-	22.7
Vitex gaumeri (*N*=3)	-	168.4	-	-	-	-	-	-	-	-	-	-	168.4
Xylopia frutescens (*N*=13 Ripe)	16.5	-	-	-	-	30.7	30.7	93.3	226.1	-	4.1	-	401.5
Zanthoxylum sp. (*N*=3)	-	1.5	-	-	-	-	-	-	-	-	-	-	1.5
Total FAI per Month	126.3	385.6	31.1	225.1	411.9	359.9	453.1	418.1	583.5	132.0	1387.2	1208.3	***5722.1***

Table 6. Fruit availability index scores for high-elevation plots in Belize, July 2008-June 2009.

Food Plant	**Jul 08**	**Aug 08**	**Sep 08**	**Oct 08**	**Nov 08**	**Dec 08**	**Jan 09**	**Feb 09**	**Mar 09**	**Apr 09**	**May 09**	**Jun 09**	**FAI**
Astronium graveolens (*N*=3)	-	-	-	-	-	-	-	-	-	4.4	-	-	4.4
Bursera simaruba (*N*=6)	49.0	49.0	49.0	49.0	49.0	49.0	61.3	49.0	24.5	-	147.1	49.0	625.1
Byrsonima crassifolia (*N*=1)	1.1	4.3	4.3	1.1	-	-	-	-	-	-	-	-	10.8
Dendropanax arboreus (*N*=6)	7.5	-	-	-	-	-	-	-	-	-	-	-	7.5
Ficus sp. (*N*=5)	-	-	19.4	-	-	-	-	16.3	12.1	-	-	-	47.7
Luehea speciosa (*N*=33)	-	-	25.2	-	-	-	-	-	-	-	-	-	25.2
Manilkara zapota (*N*=7)	-	-	-	-	6.3	-	-	-	-	114.9	108.6	90.0	319.8
Pleradenophora longicuspis (*N*=18)	-	-	-	-	-	-	-	-	-	-	241.4	40.6	282.1
Pouteria campechiana (*N*=27)	2.5	-	-	0.6	0.6	14.9	20.5	0.6	-	-	41.1	-	80.7
Protium copal (*N*=19)	-	-	58.7	-	110.4	134.7	92.9	190.4	85.8	142.8	76.2	51.9	943.9
Pseudolmedia spuria (*N*=9)	-	-	-	-	-	-	-	127.3	84.8	42.4	-	-	254.5
Simarouba glauca (*N*=8)	-	-	-	-	-	-	6.6	6.6	-	-	6.6	-	19.8
Spondias radlkoferi (*N*=5)	-	-	-	-	-	-	14.6	-	-	-	2.1	-	16.7
Stemmadenia donnell-smithii (*N*=3)	-	-	-	-	-	-	-	-	-	-	13.4	2.3	15.7
Terminalia amazonia (*N*=16)	-	-	-	-	-	-	-	33.1	-	-	732.6	-	765.7
Virola koschnyi (*N*=9)	-	-	-	-	5.4	-	-	-	-	-	29.0	-	34.4
Vitex gaumeri (*N*=11)	-	-	-	-	-	-	22.7	-	-	-	-	20.1	42.8
Xylopia frutescens (*N*=12 RIPE)	6.8	-	-	-	-	-	-	-	81.1	27.0	40.5	6.8	162.1
Zanthoxylum sp. (*N*=1)	-	-	-	-	-	-	-	-	-	-	-	0.6	0.6
FAI per Month	66.8	53.3	156.6	50.7	171.7	198.6	218.6	423.2	288.3	331.6	1438.7	261.4	***3659.5***

A fuller picture of high-elevation polewood availability was obtained by adding ripe polewood abundance scores (0-4) from the Guacamallo Bridge Road (GBR) plot and the GBR Polewood plot (Fig. 12). In these two nearby plots (< 250 m), ripe polewood peaked in March/April after a slow rise from November; macaws were present in April.

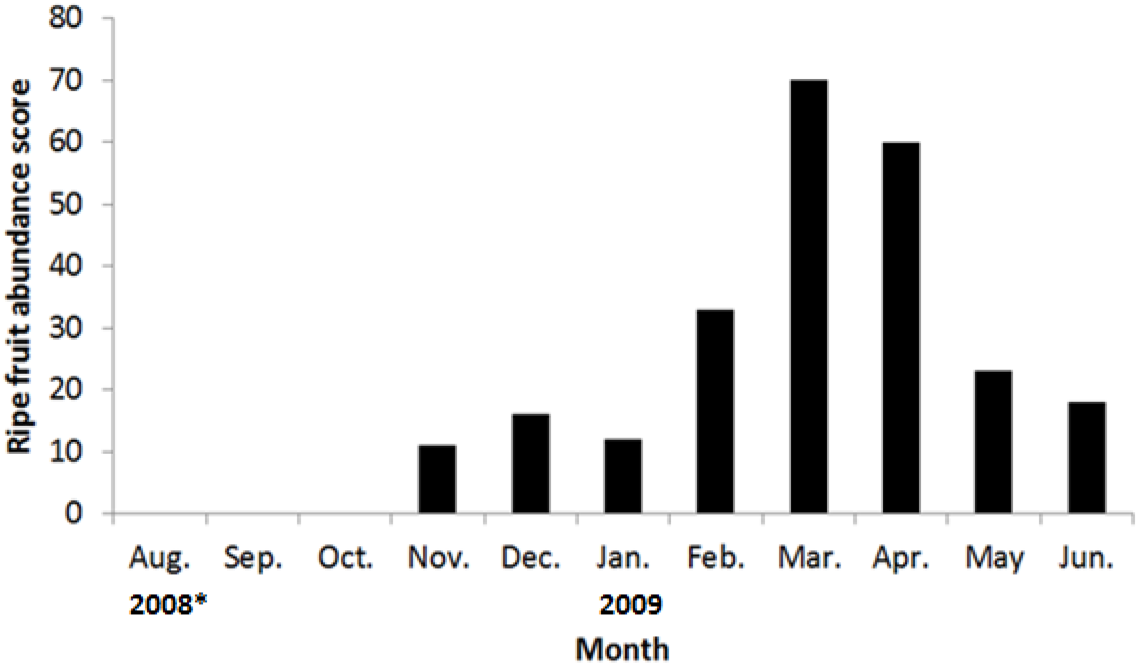


Figure 12. Abundance of ripe polewood (*Xylopia frutescens*) in two high-elevation plots, Chiquibul area, Belize, from August 2008 to June 2009. Guacamallo Bridge Road (GBR) plot ripe fruit abundance records (*N* = 10) on a total of 13 trees with fruit. GBR Polewood plot, a line transect, fruit abundance records (*N* = 106) on a total of 38 trees with fruit. * = only GBR plot sampled. Ripe fruit abundance score for an April 08 sample of only the GBR Polewood plot was 85.

For both low- and high-elevation plots, general fruit availability trended upward from July 2008 to a large spike in May 2009, continuing into June for the low-elevation plots (Fig. 13). The lowest fruit availability scores occurred July through October, during the wet season; with more fruit available in the dry season. FAI scores suggested that 22% more food was available on an annual basis on low-elevation plots (FAI = 5,722) than on the high-elevation plots (FAI = 3,660). Combining the FAI scores from both low- and high-elevation plots, there was a significant difference in the FAI scores between the wet and dry seasons (paired *t*-test: $t = 11.826$, df = 11, $p < 0.001$).

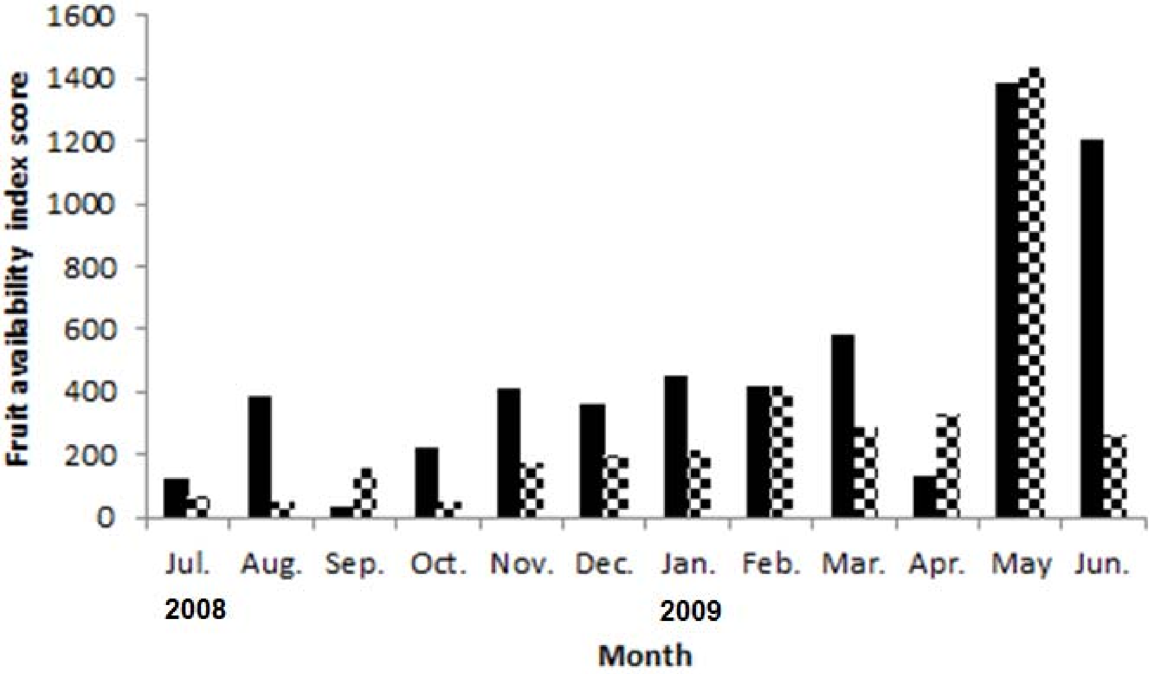


Figure 13. Fruit availability index scores for low and high-elevation phenology plots in Belize, from July 2008 to June 2009. Solid bars are low-elevation plots (*N* = 6). Checked bars are high-elevation plots (*N* = 6).

Fruit Availability from Other Sources

Data were also collected and analyzed on known or possible macaw-food species (*N* = 2820 records) in southern Belize (≤ 17° N). These data were combined with my own data to create fruit phenology charts for 67 Scarlet Macaw food species in Belize (Appendix I). Using these combined data, the annual low in the number of food species fruiting is in December with a steep rise in numbers to April and May (Fig. 14). I combined all possible records and noted seasonal and elevational differences in fruiting.

At high-elevation areas and plots in the wet season, May to October, when macaws were present, several important macaw-food plants were fruiting. Macaw feeding records indicated Fiddlewood (*Vitex gaumeri*) could have fruit from June to August and in October, so fruit may be available from June through October. Hog plum (*Spondias mombin*), likely *S. radlkoferi* (also called hog plum), has macaw feeding records from May to July and also for November and December. Red gumbo limbo had fruit of varying maturity present in all months. Records of macaws feeding on this fruit came from March and

May; macaws also likely feed on this fruit during April. From June through November, old or immature fruit may be eaten.

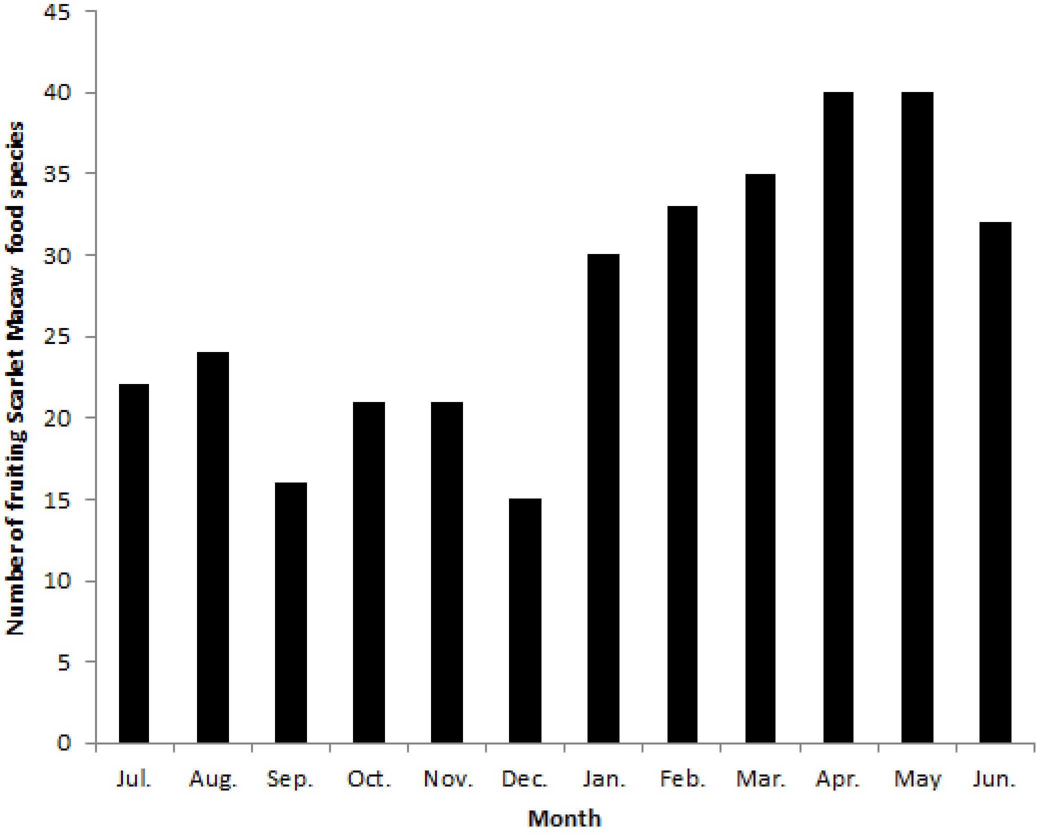


Figure 14. Scarlet Macaw food plant monthly fruiting phenology, southern Belize. Sources are from my plots and all other records.

At high-elevation areas and plots in the dry season, November to April, when macaws were present, several important macaw-food plants were fruiting. Records indicate macaws were most often seen eating quamwood from January to July. There are records of Scarlet Macaws feeding on *Ceiba* from January to May, but not in April. Copal has one macaw feeding record from N. Bol, who knew well both the plant and macaws; copal might be dismissed as a minor food, but this tree is abundant in the Chiquibul area and I have plot records of fruit from January to June. Using all possible records, I created a table showing Scarlet Macaw food availability and feeding observations in low- and high-elevations (Appendix J).

In low-elevation areas, polewood has some fruit in December and feeding records from January to March; a minor amount of fruit matures in June. The peak of ripe polewood fruit abundance in low elevations is March; in high-elevations it is March/April. My records for mo tree indicate that macaws feed on it January and March, which suggests it is also available in February. In December 2005 to March 2006 mo trees had no fruit, but from December 2006-March 2007 they were full of fruit (Sho, pers. comm. 2007), and during that period I saw several macaws eating within mo trees. I saw large flocks of up to 25 macaws feeding on mo tree in March 2009. Abundant fruit of Ekman's prickly yellow (*Zanthoxylum ekmanii*) was eaten in the Bladen area in February and March; other species of prickly yellows are likely eaten too. Details of major Scarlet Macaw food plants in Belize are in Appendix K.

SEASONAL MACAW SIGHTINGS AND DISTRIBUTION

Plot Point Counts

My field sightings totaled 743 records of one or more individuals, 24.45% of the presence records of all sightings collected; sightings were low during the point counts on the phenology plots despite placing them in areas of historic sightings (Table 7). See Appendix G for all bird species seen.

Table 7. Scarlet Macaw point count results by plot, season, and elevation, July 2008-June 2009, southern Belize.

Plot Name	**Total # of Macaws**	**Dry Season: Nov. to Apr.**	**Wet Season: May to Oct.**	**Elevation in Meters**	
				Low	**High**
Bladen	0	0	0	73	
Maya Mountain Forest Reserve	0	0	0	55	
Macaw Valley	34	34	0	233	
Guesthouse Ridge	41	41	0	123	
Snook Eddy	0	0	0	4	
Mexican Branch Trail	3	3	0	80	
Guacamallo Bridge Road	20	5	15		404
Caracol Road	21	4	17		442
Cubetas	0	0	0		643
Las Cuevas	3	0	3		570
San Pastor	1	1	0		597
Monkey Tail Trail	92	19	73		554

Macaw point count data on phenology plots were analyzed to see if macaws were more prevalent in the high-elevation plots in the May to October wet season than in the low-elevation plots in the November to April dry season. I used a Wilcoxon Signed Rank test with continuity correction; data used were not normally distributed, so I used the nonparametric test. The absolute difference of the macaw sightings by elevation between the two seasons was significant (*V* = 36, *p* = 0.014). The same data were also analyzed via a two-way ANOVA to determine relationships between elevation and season. ANOVA requires a normality assumption, not met with these data, but ANOVA is highly robust to violations of the assumption, particularly when the design is balanced by having six plot observations in each treatment (Wilson, pers. comm. 2011). Data from macaw sightings in the dry and wet seasons were not significantly different (*f* = 0.0001, df = 1, *p* = 0.990) because these birds were seen at low elevation during the dry season and high-elevation during wet season, so the two canceled. Likewise there was no significant difference in sightings of macaws by elevation in the low- and high-elevation areas (*f* = 0.483, df = 1, *p* = 0.494) because these birds were seen at low elevation during the dry season and high-elevation during wet season, so the two canceled. There was, however, an indication of an interaction between elevation and season (*f* = 3.421, df = 1, *p* = 0.079).

Non-plot Elevation Point Counts

At the low-elevation Sho's Fine Vista in Red Bank, point count sightings in the months of January to March over three years show that macaw numbers peak in February (Fig. 15). There were no macaw sightings and no indigenous sighting reports from July to November 2008. For December there were reports of a few macaws and I saw macaws in January through March, and then none in April through June. Historically there have been no macaws in the Red Bank area from April to December.

In the high-elevation Chiquibul at Guacamallo Bridge on the Macal River, monthly point counts ran from January 2008 through June 2009 with many months having no macaw sightings (Table 8). There was obvious seasonality with 88% of macaws seen in the months of July 2008, and April to June 2009 (Fig.16). Of the macaws seen, 77.1% flew upstream, 14.5% went downstream, and 8.4% flew in other directions (*N* = 83). Because most observations were conducted in the afternoon after plot work in the mornings, the upstream flights may represent macaws returning to roost or to nest sites after foraging downstream.

Macaw Sightings from Others

I sought and compiled all the Scarlet Macaw sighting records I could find that have been made by others throughout Central America; see Appendix A for sources. Those records included 2,295 presence records and 171 absence records in Belize, from the earliest mappable location in 1945 to December 31, 2009. Records within Belize came from field station logbooks that I transcribed, from published literature,

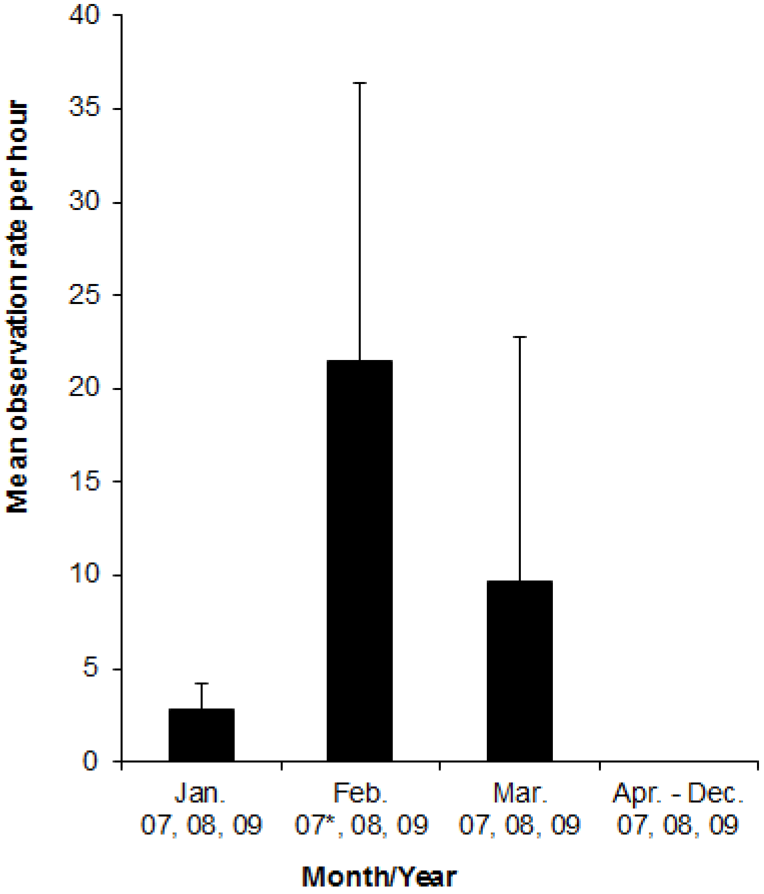


Figure 15. Scarlet Macaw sightings at Sho's Fine Vista, Red Bank Village, Belize, 2007 to 2009. Data from January, February and March with 1 SD error. * = no data Feb. 2007.

Table 8. Guacamallo Bridge point count sightings of Scarlet Macaws, Chiquibul area, Belize, 2008 to June 2009.

Month	Scarlet Macaws	Obs. Hours
Jan. 2008	3	3.08
Feb.	0	5.50
Mar.	3	9.88
Apr.	0	6.08
May*	-	-
Jun.*	-	-
Jul.	3	1.08
Aug.	0	1.50
Sep.	0	0.58
Oct.	0	0.42
Nov.	0	1.08
Dec.*	-	-

Month	Scarlet Macaws	Obs. Hours
Jan. 2009	0	1.65
Feb.	0	2.33
Mar.	0	1.33
Apr.	8	3.08
May	4	6.45
Jun.	11	3.17

* no count done.

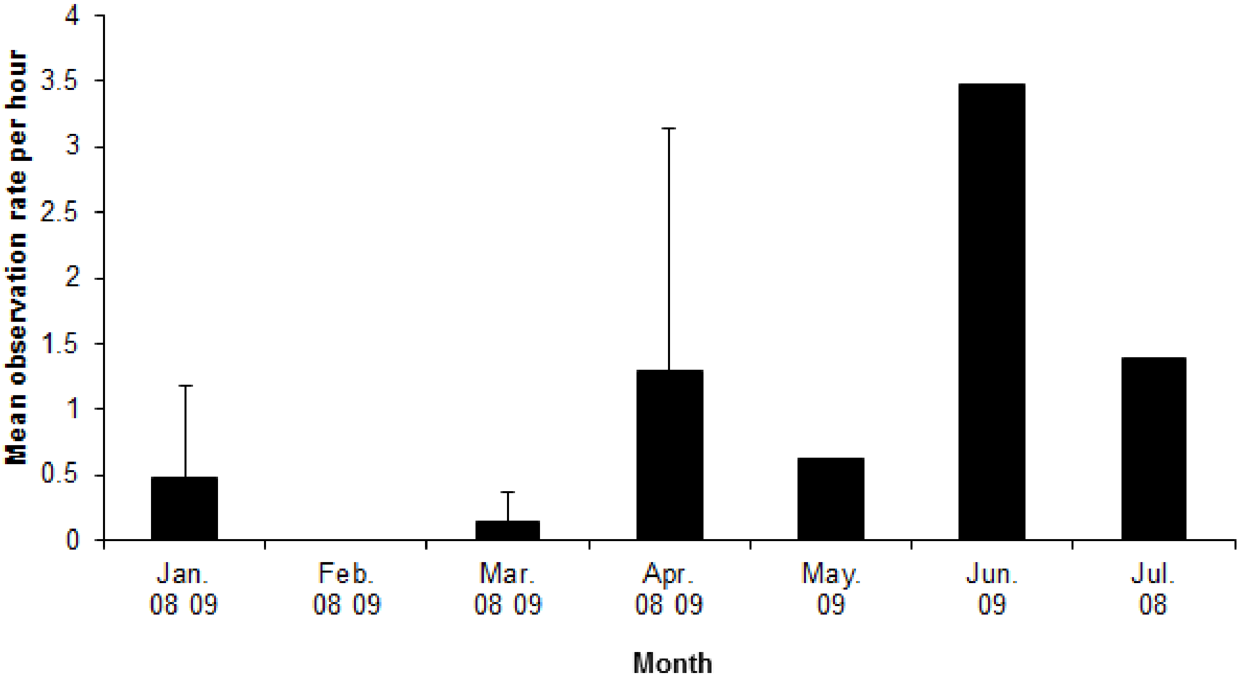


Figure 16. Mean Scarlet Macaw point count sightings, Guacamallo Bridge, Chiquibul area, Belize, 2008 to 2009. With 1 SD error for Jan. - Apr. 2008 and 2009. Data from Table 10.

or were reports or theses that had been essentially lost (see Appendix B for sources). I combined these records with my own data to produce a database that had not existed before. This database shows that macaw observations at Las Cuevas peak in June and July, with sightings in all months (Fig. 17). To see if fluctuation in number of observers skewed the data, I consulted Las Cuevas staff who stated that that was not the case, although occupancy records had been lost. To ascertain if the Las Cuevas observations were skewed, I asked FCD rangers to record all macaw sightings from their base or on patrol in the Chiquibul. Their macaw sighting data of 1.5 years, combined with my sighting data over the same time period, also show a large peak in June (Fig. 18), supporting the general accuracy of the Las Cuevas sightings, and the seasonal abundance of macaws in the Chiquibul area.

SEASONAL PATTERNS OF FOOD AVAILABILITY AND MACAW SIGHTINGS

Combining my phenology plot data with all macaw sighting data shows seasonal patterns of movement, some of which are likely due to food availability. Such patterns are reinforced and other patterns found

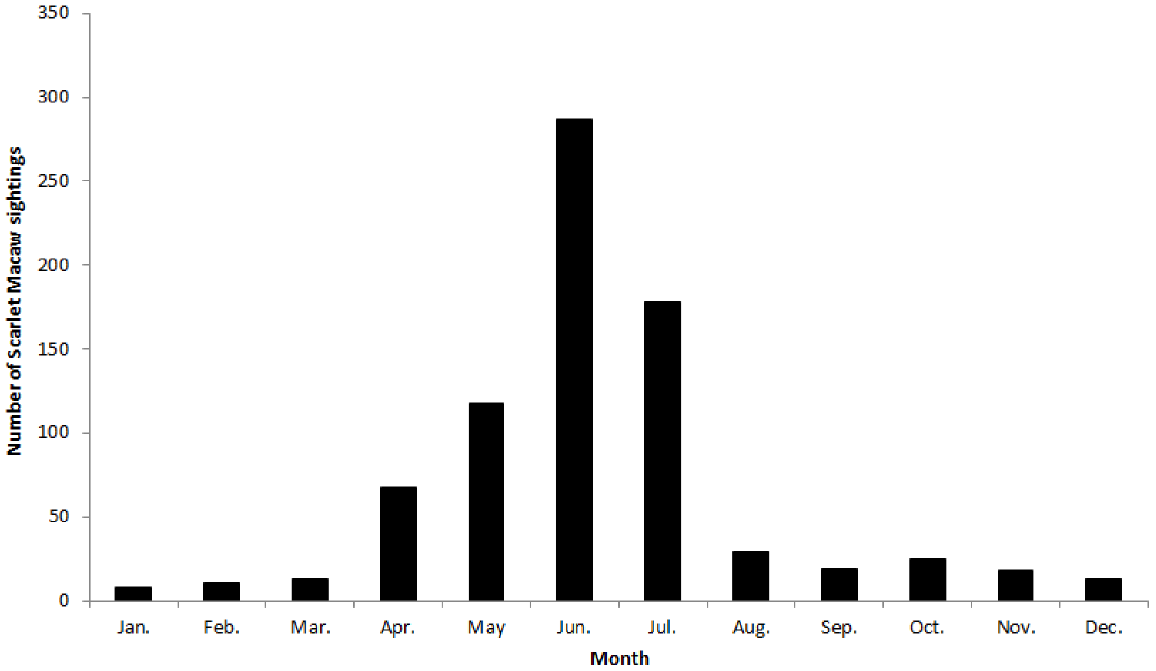


Figure 17. Macaw sightings at Las Cuevas, Cayo, Belize, from February 1995 to June 2009. Each sighting is one or more Scarlet Macaws (*N* = 787 sightings) and within 2 km of Las Cuevas. Data is from reports (Bol & King 1996; King 1998b), Las Cuevas staff, my transcriptions of sightings in the Las Cuevas Research Station logbook, and my sightings.

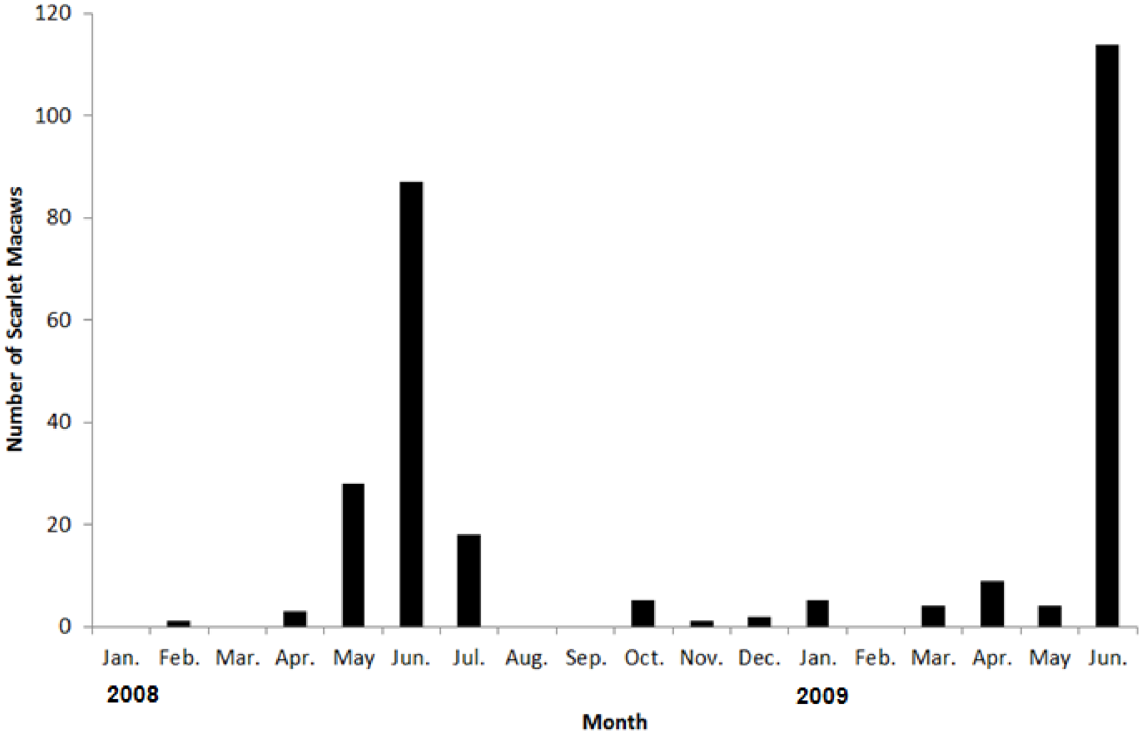


Figure 18. Macaw sightings from January 2008 to June 2009 at Caracol Junction, Cayo, Belize. Each sighting within 3 km of Caracol Junction (*N* = 281). Data from FCD Rangers, my transcriptions of sightings from FCD Ranger logbooks, and my sightings.

when historic sightings are included. I analyzed possible correlations between macaw sightings and availability of fruit in known food plants in the phenology plots. Few species showed significant positive correlations. The second highest (*r* = 0.898) was for horse's balls (*Stemmadenia donnell-smithii*) in the dry season, but it appears to be a minor food because there is only one feeding record.

Fruit availability scores within the low-elevation plots showed no significant association with the presence of macaws, seen on or off the plots, other than a strong positive correlation with the ripe polewood FAI scores from the three plots containing that plant (Fig. 19). The data analyzed for this correlation consist of two time-series variables, ripe polewood FAI scores and number of macaws. A first analysis, ignoring the time-series information of the two variables, computed Spearman's correlation (*rho* = 0.643, *p* = 0.024). A second analysis used a non-parametric bootstrap, concluding that there was a highly significant correlation (*rho* = 0.962, *p* = 0.00049) between presence of macaws and presence of ripe polewood fruit in the low-elevation plots.

Combining all low-elevation records from all sources shows that macaw feeding was focused and highly seasonal. Observer bias may impact these feeding observations from all sources because tours at Red Bank occur in January and February. However, I made 104 polewood feeding observations in January 2009, and a total of 289 feeding observations for all months of the study year. From January to March 2009 while conducting point counts on plots and at Sho's Fine Vista in Red Bank I saw macaws in Red Bank eating only polewood (*N* = 20), and mo tree (*N* = 4). Similarly, from January 10 to 23, 2007, I saw macaws eating polewood (*N* = 48), mo tree (*N* = 22), and wild annatto (*N* = 11).

As ripe polewood increased in Red Bank from November to March, so did the macaws. The macaws left Red Bank after my observation in March, the month with the highest macaw numbers of the year. Polewood and all other fruit availability also dramatically dropped after my observation in March (Fig. 20). My feeding observations and FAI data suggest that ripe polewood annually attracts and keeps macaws in the Red Bank area for an extended period of time. Data also suggest that when polewood becomes scarce, the macaws will leave Red Bank. Despite the abundance of food signified by the spike in FAI scores, mostly due to wild annatto, macaw numbers are zero in all low-elevation areas in April and May, except for a very few in Cockscomb. Fruit availability scores within the high-elevation plots show no

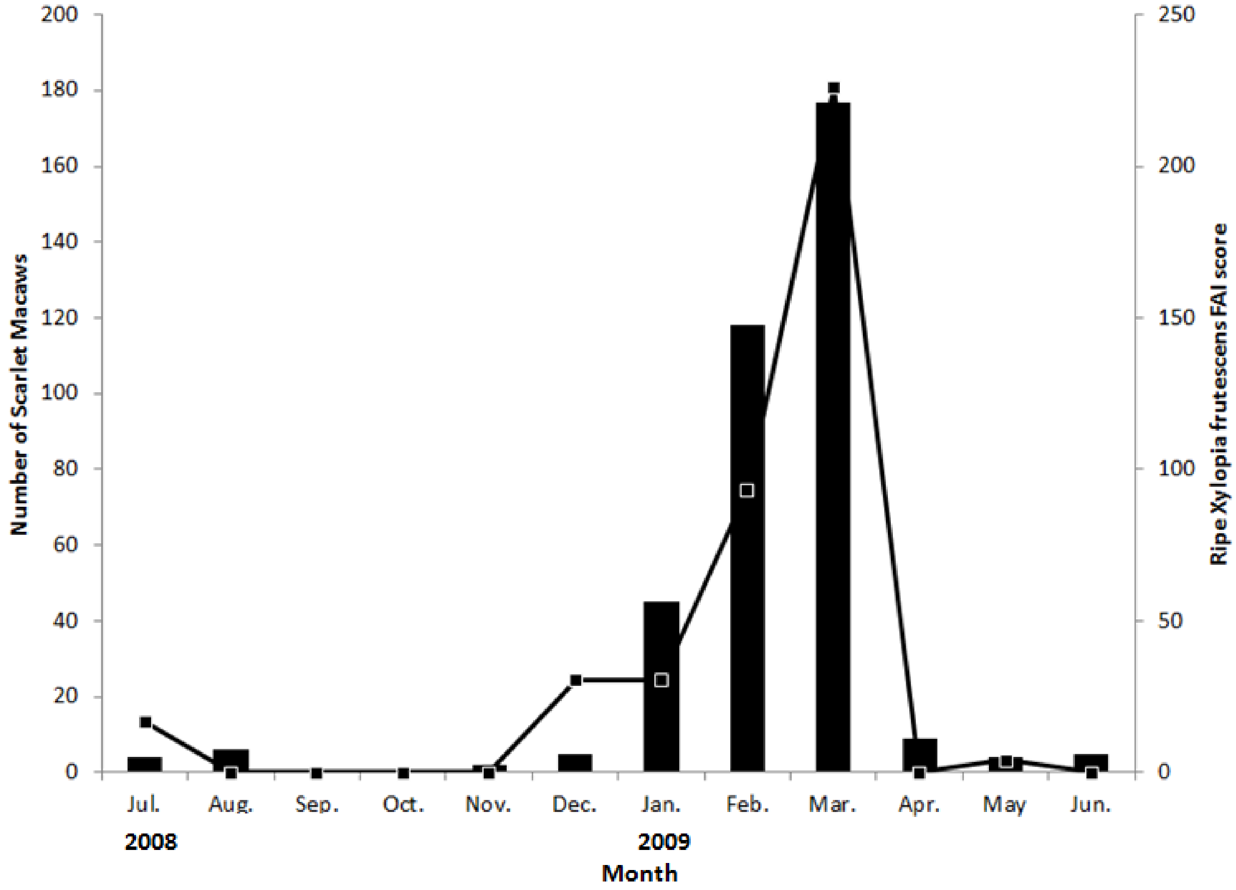


Figure 19. Comparing *Xylopia frutescens* fruit availability index scores and presence of Scarlet Macaws in Stann Creek and Toledo districts, Belize. Bars represent the number of Scarlet Macaw sightings and the line represents the FAI score of ripe polewood on three low-elevation plots: Maya Mountain Forest Reserve (Bladen area), Macaw Valley and Guesthouse Ridge (Red Bank).

clear association with macaws I observed, or with historical sightings, except for a spike in May just before the number of macaws soared (Fig.21). This spike was due to very large flocks that were counted at the FCD Guardhouse in a few days in June 2009. Individuals in these flocks were likely counted twice in a day as they flew in one direction in the morning, and in the reverse in the afternoon. These few days created very high macaw numbers for the entire high-elevation area in June 2009, but macaw numbers historically peak in June. The two high-elevation plots with polewood showed no precise temporal correlation between polewood and macaws, but a possible association is that the peak of ripe polewood occurred in March/April when macaws leave Red Bank, a month before the general jump in food availability and the high macaw numbers of May. During this study, FAI scores in both low- and high-

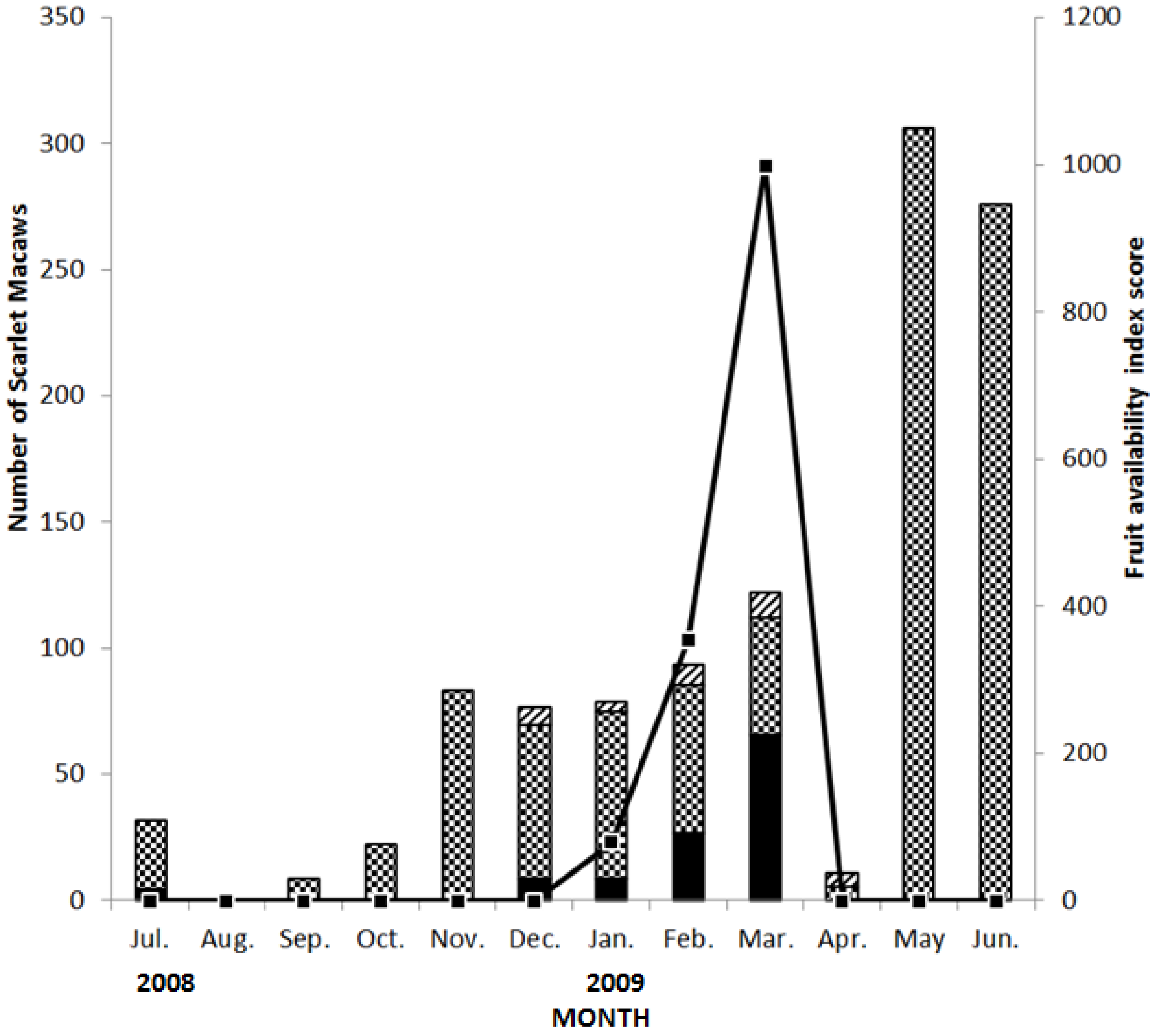


Figure 20. Scarlet Macaw presence and food availability at two phenology plots in Red Bank, Belize. Line represents number of macaws. Solid bar presents polewood. Checkered bar represents wild annatto. Diagonal bar represents white trumpet tree (*Schefflera morototoni*).

elevation plots were roughly on the same trajectory, both spiking in May. A spike in the FAI on plots in the high-elevation Chiquibul area precedes a rise and then a spike in macaw numbers a month later in June. In the low elevations, macaw numbers drop to near zero after March except for a few in Cockscomb, despite a spike in the FAI score largely due to an abundance of wild annatto fruit (Fig. 22). Including data on all known macaw sightings, from all sources and dates, shows a very clear seasonal and elevational shift in habitat through the year (Fig. 23). The historical sightings may reflect unknown bias, but still show general trends that agree with my more exacting work, the observations of others at field stations, and indigenous knowledge. In the dry season, January to March, macaws are mostly in the lower eastern foothills of the Maya Mountains, in lowland broad-leaved wet forest (Meerman & Sabido 2001). In the higher-elevation Chiquibul to the west, Scarlet Macaw sightings are year-round, but with sharply increasing sightings in March that peak in June, and then drop off. Macaws in the areas of the Macal River and Raspaculo branch of the Macal are at the edge of the lowland broad-leaved wet forest and the submontane broad-leaved moist forest, with access to 32 unique vegetation classes (Penn et al. 2004).

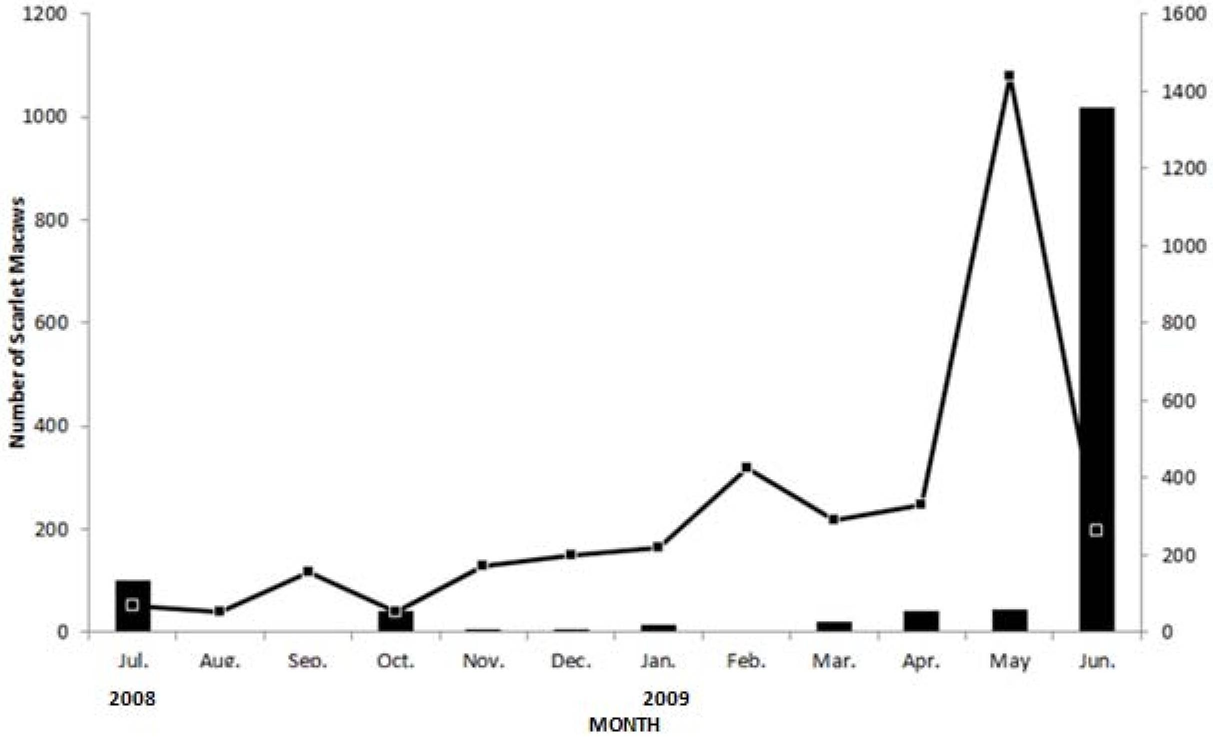


Figure 21. Fruit availability index scores on high-elevation plots and Scarlet Macaw Sightings in the Chiquibul area from July 2008 to June 2009, Cayo, Belize. Bar represents number of individual macaws sighted per month – not population per month. Line represents fruit availability index scores for the six phenology plots in the Chiquibul. Macaw data are from my sightings and FCD Guardhouse and Las Cuevas records; they do not include many FCD sightings on the Macal River or Raspaculo Branch as they were not accessible to me.

Examining all macaw sightings from all sources and dates in light of the annual breeding cycle also shows a very clear seasonal and elevational shift. During January, February, and March, macaw numbers peak in the low-elevation areas at the same time the reproductive cycle starts in the higher-elevation Chiquibul area. After March, macaws are essentially gone from the low-elevation areas, having left for the higher-elevation Chiquibul where breeding is occurring.

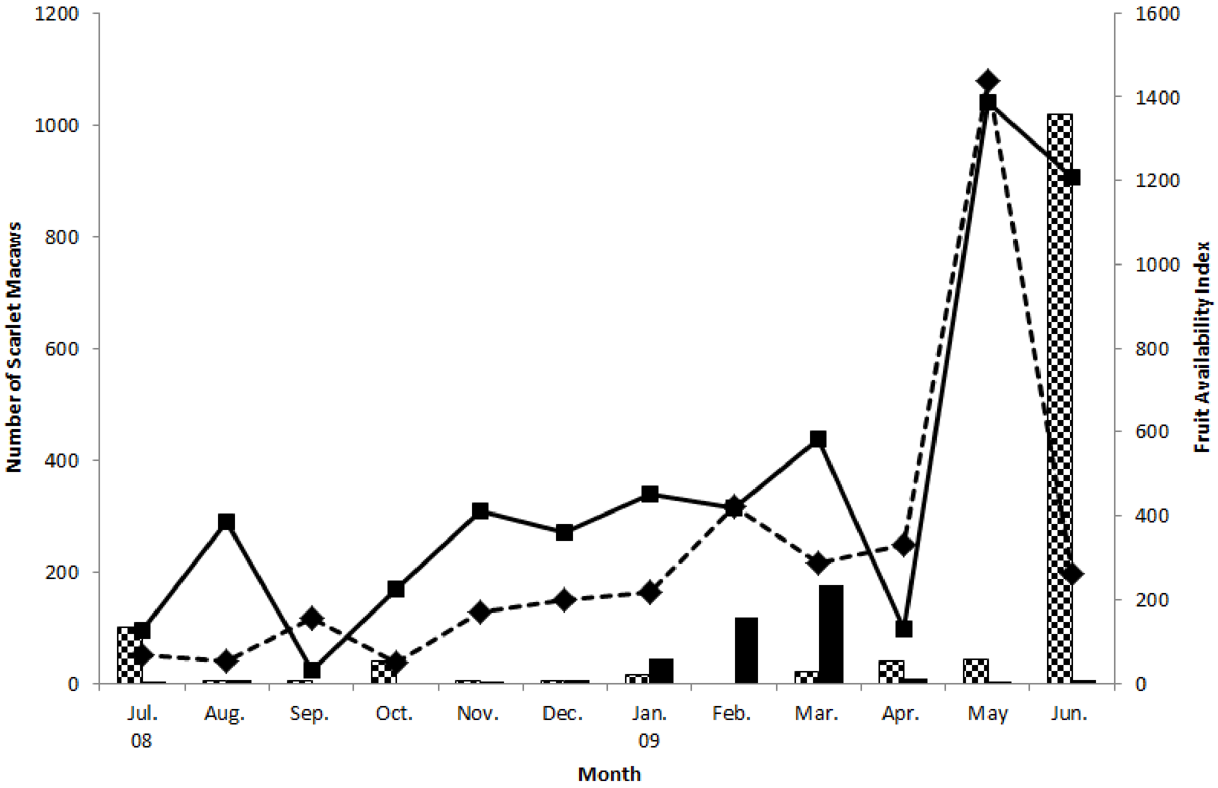


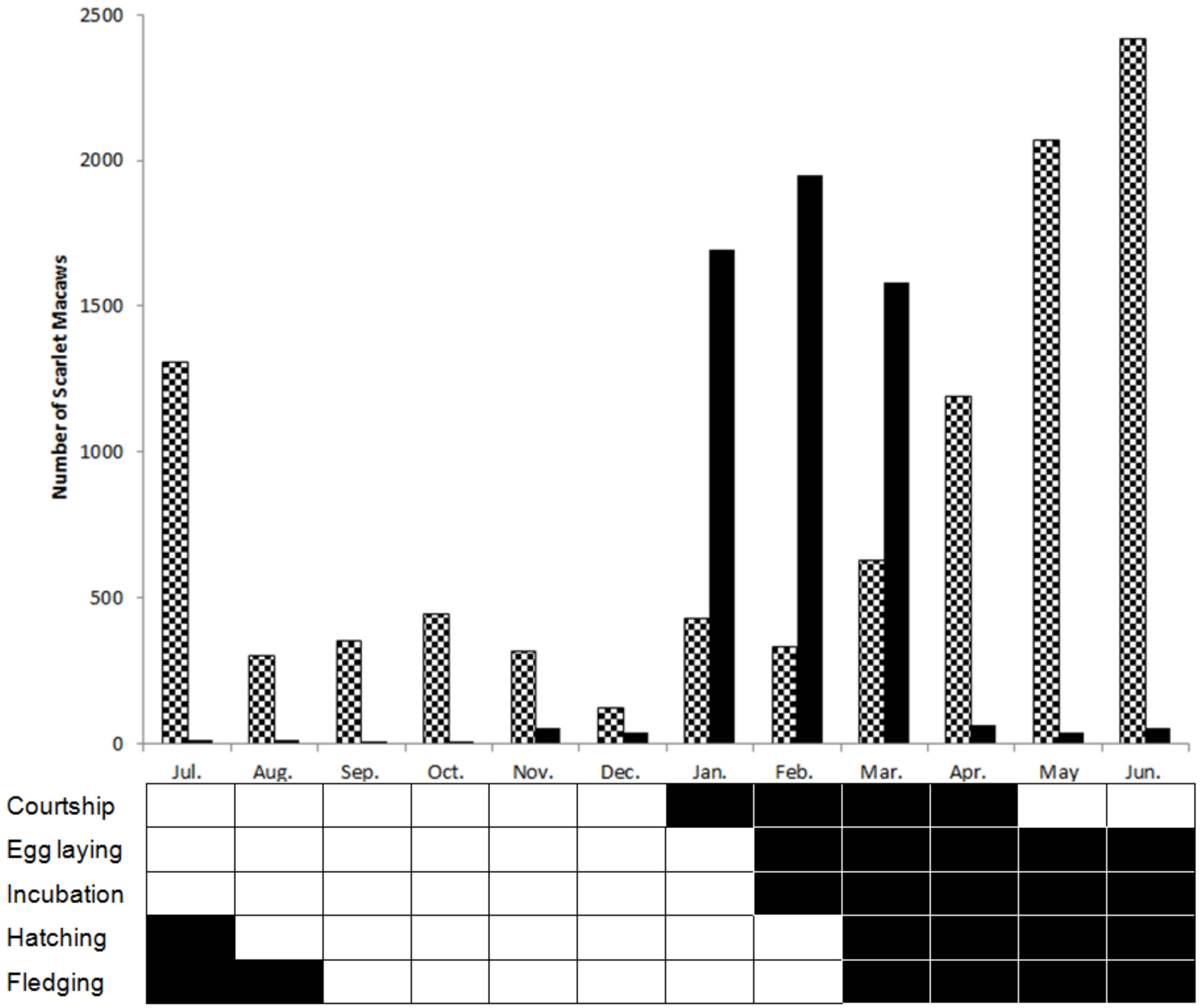
Figure 22. Scarlet Macaw sightings and food availability index scores for low- and high-elevation plots in southern Belize, July 2008 to June 2009. Dark bar is individual macaw sightings, all sources, in the low-elevation areas. Solid line is FAI score for all six of my low-elevation plots. Checkered bar is individual macaw sightings, all sources, in the high-elevation Chiquibul area. Dashed line is FAI score for all six of my high-elevation plots.

MOVEMENT BETWEEN LOW AND HIGH ELEVATIONS

Three passes over the Maya Mountains may connect the Chiquibul area (with its Macal River and Raspaculo Branch) to low-elevation areas to the east (Fig. 24). One pass leads into the western part of Cockscomb Wildlife Sanctuary (Mallory 1994; Matola & Sho 2002a), a basin drained by the Swasey branch of the Monkey River, and creates an easy route to Red Bank. This pass is at 16.797145° N, -88.722780° W (coordinates MMc), and about 666 m elevation (Google 2012); I call it Middle Pass. Evidence for flights over a second pass, which I call West Pass, comes from sightings on both the east and west sides of the crest, both approximately three km from the pass, which is at approximately 16.760258° N, -88.752310° W, and at 587 m elevation (Google 2012). From this pass, macaws may drop down into the western Cockscomb Basin following the Swasey branch of the Monkey River to Red Bank.

A third pass, which I call East Pass, is located approximately at 16.82119° N, -88.55114° W and at 150 m elevation (Google 2012). This pass is along the South Stann Creek which flows by Kilometer 12 Camp on the Victoria Peak Trail in the Cockscomb Wildlife Sanctuary. I have seen macaws flying along the river at Kilometer 12 Camp, and I have numerous records of sightings from there and upstream as well. If one follows the creek upstream from this camp it cuts around the Cockscomb ridge and goes up a large east-west oriented canyon directly behind the Cockscomb ridge and Victoria Peak. Once in this upper valley, macaws could continue over a lower area in the westernmost top of the valley at about 512 m and then drop into the upper edges of the Cocoa, a branch of the Sittee River, in the Sittee River Forest Reserve. They could move down that valley, which heads east, or they could fly into the Raspaculo drainage. Before they get to the top of the South Stann Creek valley, they could also fly north over lower passes and into the Cocoa, and then Pull Shoes, branches of the Sittee River. The upper Sittee River was identified as having good habitat (Britt et al. 2011), but there have never been sightings reported within the upper or lower Sittee River areas. I suspect that many of the macaws in the eastern Cockscomb Basin arrive from the East Pass, although other possibilities are flying northeast from Red Bank along the foothills, or flying between the east and west basins of Cockscomb. Possible passes along the crest of the Maya Mountains are higher to the south and no macaws have been seen in the Bladen River area (except at BFREE).

Macaws, from any of the above passes, may also fly southwest along the foothills from the Red Bank area, down as far south as the Bladen area. Once in the Red Bank area, macaws use a portion of the Swasey route on a daily basis, flying to a suspected roost site in a nearby tributary, Sapote Creek. Large flocks have also been recorded flying toward the northeast by others in Georgetown and from Red Bank (Meerman 1999), as well as by me. These flocks could be going to the Cockscomb Basin or its eastern foothills, all northeast of Red Bank.



	Jul.	Aug.	Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	Jun.
Courtship							■	■	■	■		
Egg laying								■	■	■	■	■
Incubation								■	■	■	■	■
Hatching	■								■	■	■	■
Fledging	■	■							■	■	■	■

Figure 23. Scarlet Macaws seen by month in southern Belize, and breeding activity in the Chiquibul. Macaw sighting data are from all sources, using all records (*N* = 3002), and from all dates to June 2009. Dark bars represent macaws seen in the Stann Creek and Toledo Districts, low-elevation areas. Checkered bars represent macaws in the Cayo District, primarily in the high-elevation Chiquibul area. Breeding activity data from along the Macal, Raspaculo, Monkey Tail and Chiquibul Rivers in the Chiquibul with most data from C. Britt (2010), chart MMc.

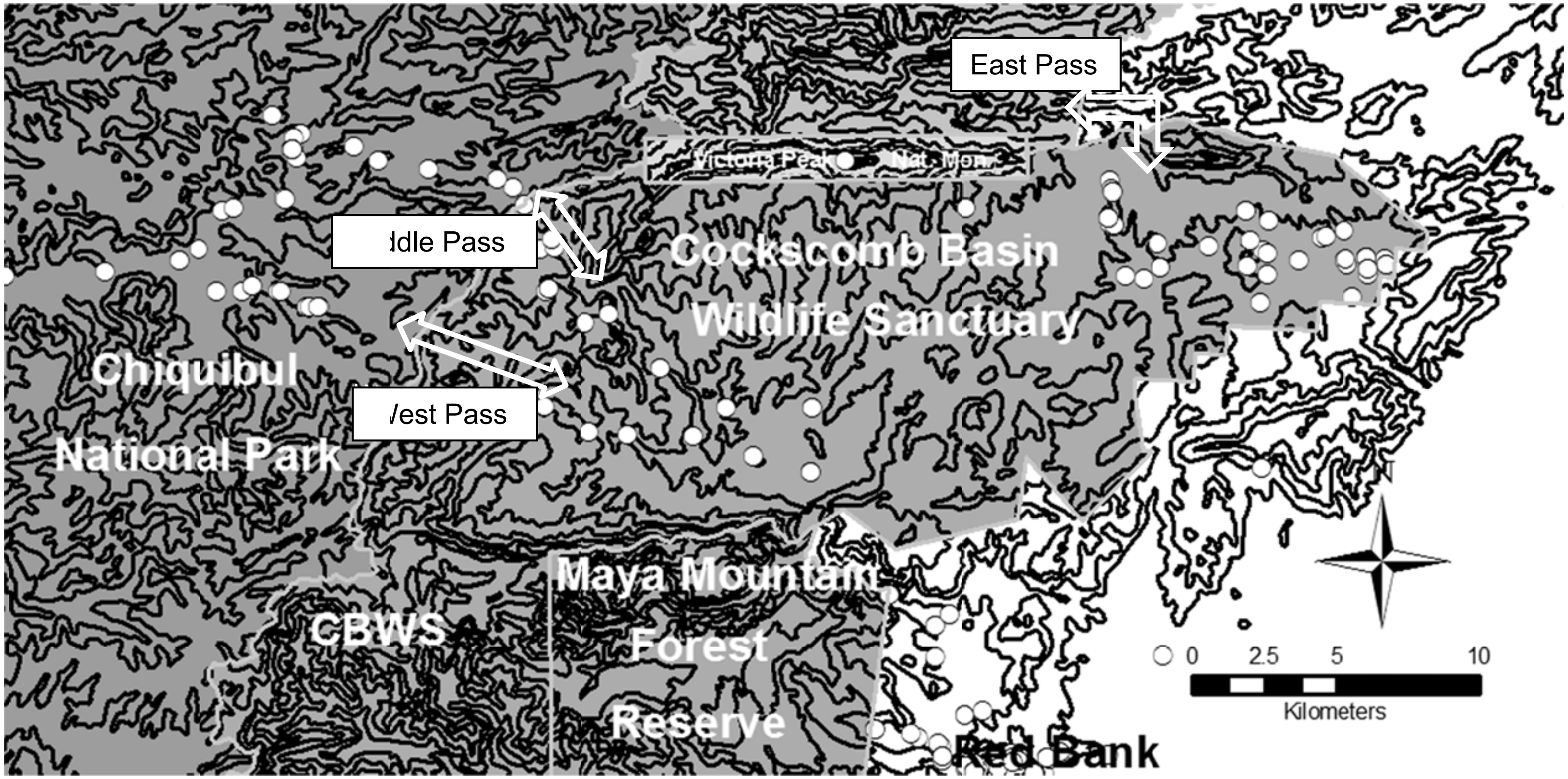


Figure 24. Sightings and proposed flight routes of Scarlet Macaws over the Maya Mountains, Belize. Points are Scarlet Macaw sightings. Arrows are proposed flight routes over the Maya Mountains.

DISCUSSION

PHENOLOGY: SEASONALITY OF FOOD AND MACAW DIET IN BELIZE

> *Phenological variation at the level of the forest community affects primary consumers who respond by dietary switching, seasonal breeding, changes in range use, or migration* (van Schaik et al. 1993).

In general, birds breed during an abundance of food for the young (Newton 2010), but that abundance may not be year-round. A study in Peru showed a significant correlation between “the number of parrot species [including Scarlet Macaws] nesting in each month and fruit and flower abundance” (Brightsmith 2006). Another parrot study found that variations in plant growth, tied to annual precipitation, were correlated with larger clutches, and more nesting success (Sanz & Rodriguez-Ferraro 2006). I found the timing and magnitude of the peak FAI in both my low- and high-elevation plots to be consistent with phenology work done in Rio Bravo in northern Belize, where the time period of greatest fruit availability was mid-April to mid-May, coinciding with the bird breeding season of March to August (Hess 1994). The midpoint of Scarlet Macaw hatching and fledging is May – the peak of fruit availability in the Chiquibul according to my phenology plot data. As the rains come in May in Belize, triggering lush plant growth at the beginning of the wet season, availability of insect protein greatly increases from dry season lows. Birds often need high levels of protein to reproduce successfully (Moermond & Denslow 1985); gall insects were found in the crops of macaw nestlings in the Raspaculo Branch (Renton 1998b, 2006).

Vegetation mapping in the Chiquibul area (Penn et al. 2004) and nationally (Meerman & Sabido 2001) was combined with sightings of macaws in Belize to determine likely macaw habitat in Belize (Wildlife Conservation Society - Guatemala 2005). WCS Guatemala had few sightings from Belize to work with, except from the Macal and Raspaculo Branch areas. Habitat quality was assumed to be best in those areas year-round, minimizing the importance of seasonal sites, such as Cockscomb, Bladen Nature Reserve, Red Bank, the BFREE area, and the Chiquibul River.

Frugivorous birds eat a wide range of seasonally available plants (Wheelwright et al. 1984; Moermond & Denslow 1985); that is true of macaws (Karubian et al. 2005; Berg et al. 2007) and of parrots (Galetti 1993; Wermundsen 1997; Renton 2001; Bjork 2004; Renton 2006). In my study of the diet of Scarlet Macaws in Belize, I found a difference in fruit availability index scores between the low eastern area and the high Chiquibul area, and between dry and wet seasons.

In low-elevation areas, wild annatto was available essentially year-round and horse's balls all months except June to August, although neither fruit may have been at the macaws' preferred stage of ripeness throughout that time period. At Red Bank, polewood, wild annatto, and mo tree were the macaws' chief foods; when ripe polewood disappeared in March, so did the macaws. Rather than switch foods, they appear to switch locations to where polewood is again ripe and abundant: March/April in the Chiquibul. With many other food plants available in the Chiquibul, macaws there seem not to concentrate their feeding on polewood in the same way they do in Red Bank.

In the high-elevation Chiquibul, I observed or found reports of red gumbo limbo fruit in all months. I compiled reports of macaws feeding on quamwood, a legume likely high in protein that blooms only once a year in January and February, the dry season; as is typical of many Central American trees (Janzen 1967; Croat 1975; Lobo et al. 2008). When quamwood seeds are gone, by July at the latest, the macaws must switch to other foods. Chaya, available almost year-round in its various species, is important for nestling macaws in Belize (Renton 1998b, 2006).

Despite information gaps on plant fruiting in Belize, there may be a few species that are important but only seasonally available, possibly keystone (Terborgh 1986) or fall-back food plants (Furuichi et al. 2000). In the Chiquibul a number of important food resources were not in my phenology plots because the plots were not in riverine areas frequented by macaws. Quamwood common in the Macal and Raspaculo drainages, is likely a keystone plant for macaws, critical for nesting and feeding nestlings (Renton 1998b, 2006). In the Chiquibul, fig feeding observations have been made in the Macal and Raspaculo drainages: (*Ficus glabrata*) (Mallory & Matola 2002b), and (*Ficus* sp.) (Minty 2001). *F. insipida* is noted as common in riverine habitat along the Macal at Guacamallo Bridge (Urban et al. 2006), and *F. glabrata* and *F. guajavoides* are common in riparian margins high in the Raspaculo drainage (Brokaw 1991). Figs are eaten by Scarlet Macaws in Guatemala and Costa Rica, where most diet research has been done, and are likely eaten throughout Central America. Known as keystone species in other tropical sites (Terborgh 1986), figs are likely available year-round because of asynchronous fruiting (Janzen 1979).

Bri bri (*Inga vera* ssp.), another presumably protein-rich legume, has the potential to be an important macaw-food. It was observed being eaten in the Macal River area (Mallory & Matola 2002b;

pers. obs. 2009), and was very abundant in the Macal's riverine community around Guacamallo Bridge (Urban et al. 2006); *Inga* sp. was noted as common in riverine habitat of the Raspaculo Branch (Brokaw 1991).

Globally, three plant families are very important for all frugivores: Arecaceae (palms), Burseraceae (gumbo limbo), and Lauraceae (wild avocado) (Snow 1981). Arecaceae is a known keystone plant family in the tropics (Terborgh 1986). For macaws in Belize, cohune palm may be an important backup or keystone species because it has year-round fruit in Rio Bravo to the north (Hess 1994); it likely has year-round fruit in southern Belize as well, where it is quite abundant. Cohune palms bear large clusters of oblong fruits, 4-7 cm long, 3.3-4.5 cm in diameter (Henderson et al. 1995), with extremely hard endocarps. Because macaws can not penetrate that endocarp, cohune palm was not sampled in my research. I did find references to macaws eating the epicarp, the outer layer (Bol & King 1996; King 1998a; Matola & Sho 1998; Renton 1998a, 1998b; Minty 2001), and I observed that behavior once. Macaws also ate botan palm (*Sabal mauritiiformis*) (Bol & King 1996), which has small fruit (0.8-1.1 cm) (Henderson et al. 1995).

Burseraceae contains two species common in the high-elevation Chiquibul that have feeding records and are likely important macaw-food plants: *Bursera simaruba* has fruit available year-round, and copal (*Protium copal*), nine months of the year. In the low-elevation areas, false copal fruit is available for eleven months, with no feeding observations. Lauraceae species eaten by macaws include *Licaria peckii* and *Nectandra* sp. in Belize, but this family has very few feeding observations compared to Costa Rica; there it is important for large avian frugivores (Skutch 1969; Wheelwright 1983; Wheelwright et al. 1984; Powell & Bjork 1995).

Aside from quamwood, if there is a keystone plant species in the macaws' diet in Belize, the most obvious is polewood, the dominant food in the low-elevation areas. When polewood fruit is low, or nil, macaws do not come to the Red Bank area (Romero 2004), and point counts and phenology work in Red Bank showed that macaws left when polewood fruit precipitously declined. At Red Bank, macaw numbers grew in significant correlation with polewood from January to March, but plummeted when April FAI scores for both polewood and wild annatto dropped to nil. In May in the high-elevation Chiquibul, FAI scores soared to an annual high of 1439, and macaw sightings were also high. It seems clear that a lack of fruit in the low-elevation areas and Red Bank, combined with abundant food in the Chiquibul, created circumstances strongly favoring elevational migration.

MIGRATION OF SCARLET MACAWS

In northern Central America, Scarlet Macaws have been observed making seasonal movements that involve elevational shifts; such behavior has not been recorded in southern Central America. As one moves north, more pronounced dry and wet seasons make fruit more seasonal. Greater seasonality can lead to partial migration, or eventually to migration of an entire population between breeding and nonbreeding locales (Cox 1985). Analysis of North American migrants showed that as one moves north, numbers of wintering species decrease approximately 1.1% per degree of latitude (Newton & Dale 1996a), likely due to lack of food and lower temperatures found farther north. A similar trend was observed in analysis of migrant species in western Europe (Newton & Dale 1996b). If these trends are extrapolated to Central America, a migrational gradient may be seen in the differences between migration in the northern and southern ranges of the Scarlet Macaws' distribution.

In Panama, there is no information concerning Scarlet Macaw movements other than daily movements on Isla Coiba (Wetmore 1957). In Costa Rica, Scarlet Macaws in the Carara area were said to stay in the area (Vaughan 2002), but local inhabitants in the mountains northeast of Carara told one investigator that Scarlet Macaws appeared when the guanacaste (*Enterolobium cyclocarpum*) seed pods matured, and the macaws left shortly thereafter (Boyd, pers. comm. 2011). For Nicaragua, little is known of the daily, seasonal, or elevational movements of these birds, but in the Mosquitia (Moskitia) area they may move seasonally from pine savanna (where they nest), to upland areas with more food trees. In Honduras, Scarlet Macaws in the Mosquitia area show such behavior by moving from lowland pine savanna in the Rus Rus area (where they nest) to upland broadleaf forest (Portillo Reyes et al. 2004). Scarlet Macaws move seasonally from their lower breeding grounds to feed on pines in the mountains (Bonta, pers. comm. 2006), and move from the lower El Paraiso department to the higher Olancho department (Thorn 1991). In Guatemala, the entire population of Scarlet Macaws in the somewhat higher-elevation Petén annually move approximately 80 km to lower-elevation habitat (Rodas et al. 2001; Moya & Castillo Villeda 2002; Rodas 2002); if the distance were greater this might be called annual migration. In Mexico, Scarlet Macaws were reported to be moving seasonally between the mountainous Oaxaca area and the low area of Atlantic Mexico (Binford 1989); and may still occur with sightings of Scarlet Macaws “at least seasonally” near La Gringa, Oaxaca, elevation 656 m (Peterson et al. 2003). Scarlet Macaws seasonally visited the mountainous Chiapas region to feed on *Ostrya mexicana* [now *O. virginiana*] (Rovirosa 1887). In Chiapas, *O. virginiana* occurs from 1728 m to 2356 m (N = 3) (Tropicos.org 2010) and is noted as an upland species (Record & Hess 1943).

Movements of Scarlet Macaws in Belize

In Belize, my research has shown that most of the population of Scarlet Macaws are seasonal elevational migrants following a seasonal pattern of fruit abundance. Annually, some macaws fly from the high-elevation Chiquibul to the low-elevation Maya Mountain foothills (and especially Red Bank), and then return.

Although it can include a component of elevational migration, dispersive migration does not completely describe all Scarlet Macaw movements in Belize. Newton (2007) says that dispersive migration is “not directional” (but these macaw movements are), that “all or most individuals remain year-round in their breeding area” (few macaws remain in their Chiquibul breeding area), and that movements are short “from a few to tens of kilometers” (possibly applicable to these macaws). The general term of *migration* does describe the movements of Belize’s macaws, which make “regular return movements, at about the same times of year, often to specific destinations” (Newton 2008). This is not the more familiar annual long-distance movement in which an entire population moves between distinct breeding and wintering areas on an annual basis. In Belize the migratory movements are short, and not all the birds migrate, some staying in the Chiquibul to breed beginning in December and January. Macaws from the lower-elevation eastern foothills may fly back to the Chiquibul breeding grounds in March or April, but evidently not for breeding. Britt et al. (2011) concur, mentioning non-breeders in the Red Bank area, while breeders stay in the Chiquibul area.

Combining the results of my research with the work of others, I trace the movement of Scarlet Macaws throughout the year and provide evidence that this movement is:

Partial migration - because macaws are present at low- and high-elevations during the same months. Those most likely to migrate would be those too young or too old to breed, or those unable to compete successfully for a nest cavity or food.

Facultative migration - due possibly to changes in environmental conditions, and not obligate. Migrants leave the only known breeding grounds at the beginning of the breeding season.

Elevational migration – the movement clearly has an elevational component, with some macaws annually flying from the western high-elevation Chiquibul to the eastern low elevations, and then returning to the Chiquibul.

Why Breeders Stay in the Chiquibul

Nest cavities for macaws have been concentrated along major rivers in the Chiquibul region (Renton 1998b; Minty 2001; Matola & Sho 2002a; Britt 2010d, e; Britt et al. 2011). These nest concentrations may be influenced by anthropogenic habitat destruction surrounding the Chiquibul and in upland areas within it (Bird 1998). The upland areas are still subject to logging (pers. obs. 2009). King (1998) found very few large dead trees in the Chiquibul, and noted that live trees tended to be larger near rivers. He suggested that macaws nest in riverine areas primarily because large trees there could have cavities large enough for nesting. My literature search led me to believe that the major nest tree, quamwood, was limited to the river valleys, and so were the nests, but quamwood is abundant throughout the Chiquibul (Bol, pers. comm. 2009; pers. obs. 2009). Plenty of quamwood trees were seen on a Lighthawk overflight:

> Down the Macal River, up Blossom Berry Creek, down the Raspaculo Branch, up Monkey Tail Branch, and down the Chiquibul Branch … there was a large number of quamwood trees available for macaws to search for nest cavities (Britt 2010a).

Another possibility is that few have searched for nests elsewhere. Two nests were reported near Las Cuevas Field Station (Bol, pers. comm. 2005) and a few others elsewhere, on the spine of the Maya Mountains (Russell 1964), and in the Cockscomb basin (Kamstra 1987). Before protective status was conferred in 1984, logging in the Cockscomb basin provided increased access to hunters who brought chicks out of the area (Saqui, pers. comm. 2009). In 1993, a possible nest in the Cockscomb was observed (Kamstra, unpub. 2001), but there have been no reports of nests since.

Breeding macaws start nest inspection in the Chiquibul in January and egg laying in February (Minty: Britt 2010a, b), but nestlings have been observed as late as July 25 (Mallory & Matola 2002b). Satellite tagging of three female Scarlet Macaws showed that all three “continued to return and utilize area around the nest for the entirety of the 8 months" (Britt et al. 2011). If parent macaws were at the nest site in the previous December and busy at the nest through May (when the tagging occurred) these breeding macaws evidently stayed at or near their nest cavities throughout the year. None of the satellite locations were near or over the Maya Mountain Divide (Britt et al. 2011).

One reason why breeders stay in the Chiquibul area is the abundant food for nestlings, although when breeding started in December and January the FAI was low; this is in line with the observations of Loiselle & Blake 1991b that "frugivore breeding was seasonal at all forests and occurred when ripe fruit abundance was low." My Chiquibul phenology plots showed the highest annual fruit availability in May and June, when young nestlings are fledging and in need of easily foraged and abundant food. In general it is understood that tropical birds will time fledging to coincide with peak food production (Skutch 1950; Poulin et al. 1992), but weather changes due to El Nino or La Nina have changed food resource phenology for Lilac-crowned Parrots (*Amazona finschi*) in Mexico (de la Parra-Martinez & Renton 2010).

Another factor may be a scarcity of tree cavities large enough for nesting and roosting. There is some debate about whether nest cavities in the tropics are rare (Newton 1994; Cornelius et al. 2008; Cockle et al. 2010) or common (Boyle 2008b). Tropical areas have 2.5 times more cavity nesters than temperate areas and about the same number of excavating species (Gibbs et al. 1993). Large dead trees may have large cavities suitable for macaws to use as nest or roost sites and large live trees can develop suitable cavities when limbs are torn off by winds and the heartwood is exposed to decay. In Guatemala, a study in roughly similar habitat showed only 11% of large trees (*N* = 243) had cavities suitable for nesting and of those, 7% were invaded by other species, leaving only nine active Scarlet Macaw nests (Villeda 2001).

Nest sites are rare in Belize (Renton 1998b) and have become more so due to flooding associated with Chalillo Dam that destroyed known nest sites (Minty 2001); artificial nests placed as mitigation were not used (pers. obs. 2009). A few possibilities for this failure are that the highly visible white plastic tubes could be detected easily by predators (White et al. 2006), that the nests were placed in breeding territories that were already occupied, and that there was no shortage of nest cavities, perhaps because of drowned trees developing cavities and nest sites (pers. obs. 2009).

Breeding adults may stay in the Chiquibul area year-round to protect rare nest and roost cavities and associated territory. By staying on the breeding grounds macaws gain a competitive advantage in nest and territory defense (Fretwell 1980; Gauthreaux 1982), and a reproductive advantage according to the "arrival-time" hypothesis (Ketterson & Nolan 1976). Most migratory birds have high site fidelity and consistently return to the birth site (Fretwell 1980; Berthold 2001; Newton 2010). "Reuse of nest sites is common in passerines (up to 50%), with waders up to 80% and up to 90% for raptors" (Newton 2008). One study showed that "site fidelity of parrotlets" was strong, with 95% of adults moving < 500 m in consecutive years (Sandercock et al. 2000). In Guatemala, repeat nest use by radio-tagged Scarlet Macaws has been observed (Rodas et al. 2001). In Belize, three tagged breeding females stayed near their respective nest territories:

> They did not relocate to another roosting site in a different area. This exhibited site fidelity may be a result of increased competition for nesting sites, may indicate the overall quality of the habitat surrounding the nest sites, or reflect parents' unwillingness to move into other areas with young (Britt et al. 2011).

Macaws also use nest cavities as roost sites. In Mexico, macaws preferred nest cavities as the night roost site, whether in breeding season or not (Iñigo-Elias 1996). Iñigo-Elias (1996) and Arroyo (2000) both found that some macaws also had favored roosting places apart from nests.

Fewer predators in higher-elevations may also be a factor in explaining the movement of tropical birds to higher-elevations to breed (Boyle 2008a). In Belize, breeding macaws simply stay at high-elevation, but elevation does not deter predators in the form of Guatemalan nest poachers.

I speculate that any breeding east of the Maya Mountain Crest, as is possible at Cockscomb, could be a remnant of a population that formerly bred in low elevations. Pre-colonial breeding grounds could have included the now heavily logged Atlantic coast pine savannas. In Honduras and Nicaragua, macaws breed in these coastal savannas which are extensions of those found in Belize (Howell 1972; Portillo Reyes et al. 2010a). Reliable contemporary oral accounts place Scarlet Macaws in northern Belize in the 1940's: Scarlet Macaws were sought for pets from the August Pine Ridge (savanna) and Gallon Jug areas (upland) of Orangewalk District (Urbina, pers. comm. 2010). Other accounts cover southern Belize:

> Dora Weyer (pers. comm.) [Founder of the Belize Audubon Society] reported that Scarlet Macaws used to occur in the coastal pines east of the [Maya] mountains. Charles Wright (pers. comm.) [of *Land in British Honduras*] reported that every April in the 1970's a few

> pairs [of macaws] flew in from the southwest to the Big Falls area [Toledo District] apparently to breed in a stand of gigantic pines near the Rio Grande River. After the stand was cut in 1985-86 the birds no longer returned" (Mallory & Matola 2002a).

In southern Belize, macaws could have flown down in December to breed in the low elevations because of that area's abundant food in January through April. They might then have flown back up in May and June for the abundant food in the Chiquibul. In northern Belize a similar movement could have occurred between the lower savanna and the higher Gallon Jug area.

Elevational migration is a common occurrence among tropical birds (Loiselle & Blake 1991a, 1992; Powell & Bjork 1995). A latitudinal shift north to obtain better food is posited in the general theory of tropical origins for migration and movement (Rappole & Jones 2002); this is the equivalent of movement up in elevation to the Chiquibul. Stiles (1988) uses the term "altitudinal migration" when describing elevational migration: "an altitudinal migrant shows a pronounced decrease in abundance at one altitude, at the same time that it shows a roughly corresponding increase at a different altitude." My research shows that this spatiotemporal change in abundance occurs in March through April when macaws leave the lower elevations and Red Bank to move to the higher-elevation Chiquibul. I also documented few Scarlet Macaws in the higher-elevation Chiquibul area in January and February, the same months when their numbers dramatically rose in Red Bank. Britt (pers. comm. 2010) suggests an emptying out of the Macal, Raspaculo, and Monkey Tail drainages in late January to February:

> Two weeks ago (Jan 25-29) [2010], we kayaked five days down the Macal from upper headwaters to the [Chalillo] dam. Counted a total of 130 macaws. I believe that 13 were juveniles. Interesting note: just spent two days on a joint patrol. On the 9th [of February 2010], we took the motor boat up the reservoir [up the Macal] and then kayaked up Blossom Berry [Creek] for 3 hours up and 2 hours back. No macaws. From Blossom Berry to Raspaculo we observed a single pair. We camped on the Raspaculo. Nothing observed. On the 10th, we took the boat up the Raspaculo as far as possible, maybe 750 m below Chapayal, then I kayaked 3 km up Monkeytail and back in a day. I only observed a group of 3 macaws at my turnaround point. That was it for the rest of the trip. Quite a contrast from the trip only two weeks before.

The seasonality of macaws in the Chiquibul area has not been well documented until now. Reports of work at Las Cuevas in the Chiquibul area in 1995-1996 (Bol & King 1996; King 1998a, b) were not well distributed and essentially lost until I established contact with the only coauthor of the work who had a manuscript copy (King). Their observations of seasonal abundance of macaws in the Chiquibul agree with my research. My observations strongly suggest that some Scarlet Macaws seasonally move between the higher Chiquibul area and the lower-elevation Maya Mountain foothills, with large groups at

Red Bank. There are reliable reports of Scarlet Macaw “scouts” arriving in small numbers in the low-elevation areas in November and December (Sho, pers. comm. 2009; Bech, pers. comm. 2012) to determine fruit abundance. Recent work in South Africa indicates that parrots are able to do “aerial reconnaissance” to determine fruit abundance (Boyes & Perrin 2010).

The term partial migration best describes macaw movements in Belize. That is, “some individuals remain year-round, while others from the same breeding areas leave to winter elsewhere” (Newton 2010). If it is breeding macaws that stay in the Chiquibul area, then the macaws that leave in January and February may include recent young and birds up to 4 years; in captive birds reproductive maturity is 2.5-4.0 years (Abramson 1999). The individuals that migrate would be non-breeders, those not capable of keeping a nest cavity and territory, specifically the young of the year, immature juveniles from previous years, and those birds past their competitive and reproductive prime. Although it would assist dispersal of fledglings, such movement is not immediate post-fledging dispersal since fledging occurs several months before arrival of macaws in the low elevations.

According to Newton (2008) “Where only part of the population leaves the breeding area, the commonest pattern is for juveniles to migrate in greater proportion, to leave earlier and return later, and to winter further from the breeding areas than adults.” The term differential migration primarily refers to entire, not partial, migrations (Berthold 2001; Newton 2010). Gauthreaux (1982) listed numerous studies of partial migrants in which the juveniles were predominately migrant while the adults were predominantly resident. If juvenile Scarlet Macaws do migrate and adults stay, then both terms apply. According to one definition of differential migration applied to partial migration, “some classes of a population migrate while others do not” (Ketterson & Nolan 1983). Newton (2008) generalizes that subordinate age groups, like these non-breeding macaws, are more likely to migrate than dominant birds. Several environmental and behavioral factors affect which macaws stay in the Chiquibul and which leave.

The “dominance” theory states that older or larger birds can outcompete younger and smaller birds in times of adverse environmental conditions (such as food or nest scarcity) so the non-dominant birds migrate elsewhere (Ketterson & Nolan 1976). A scarcity of cavities for nests, doubling as roost sites, leaves some individuals more vulnerable to predation and weather (Rappole 1995), and so may provide incentive to migrate. Nest inspections in December start the breeding season for macaws in the Chiquibul and in that month macaws begin to be seen again in low-elevation areas. This movement may be because the onset of breeding brings on increased territoriality and competition for roosting sites and nest cavities. Newly fledged macaws encountering agonistic behavior for the first time in the first breeding season are likely to have increased stress-related hormones which are related to migratory movements (Wingfield 2003). Differential migration “may be due to competition”(Bairlein 2001).

Nest site competition among parrots can be “intense” (Brightsmith 2005) with “possession of the nest-hole … one of the most frequent causes of fighting between conspecifics,” and nest defense begins months before egg laying (Collar 1997). In Guatemala, three incidents of intraspecific competition for nests by Scarlet Macaws were noted in 2001 and five in 2005 (Moya & Castillo Villeda 2002). Rodas et al. (2001) observed a radio-collared Scarlet Macaw female return to her nest cavity from the previous year and, finding it already occupied by a pair of macaws with three eggs, she smashed the eggs, and the pair then abandoned the nest. The radio-collared female then laid her own three eggs. In Costa Rica, just outside the Carara National Park, I watched nest defense behavior by Scarlet Macaws; both adults would stand in the nest cavity entrance and screech loudly when another pair landed in the nest tree, and then fly after the fleeing interlopers loudly squawking all the while. In Belize, there was a “high degree of territoriality around nest cavities...and occasional beak and claw fights” with intruding macaws. Some nests were in use during breeding season by non-breeders (Renton 1998b). In Mexico, mated Scarlet Macaw pairs may still use and defend the nest cavity as a roost site even out of the breeding season (Iñigo-Elias 1996).

Nest territories are also defended, suggesting that behavioral spacing requirements may limit the number of possible nests in an area. In two parrot studies with nest cavity reuse rates of 16% and 42%, pairs defended not only the nest cavity, but others nearby, which could be used in coming years (Salinas-Melgoza et al. 2009; Rivera et al. 2012). In Peru, a study of Blue-and-yellow Macaws (*Ara ararauna*) showed that 64% of potential nest cavities went unused because of the protective behavior of nesting pairs (Renton 2004).

In addition, as breeding season begins, non-breeders may encounter newly vigorous defense of heavily used riverine foraging and flight paths. The “limited foraging opportunities” hypothesis posits missed feeding possibilities and thus a move downslope to more abundant food (Boyle 2011), such lack of food could be one of the factors influencing movement out of the Chiquibul.

Why Do Some Macaws Leave the Chiquibul?

It might seem unlikely that food limitation due to intraspecific competition could be a factor because macaw numbers are surely smaller than in the past and the current habitat appears to be lightly used by so few macaws. In general, migrant birds vacate areas due to food scarcity at the first site to take advantage of abundant food at a new location, especially if the cost of migration is low and the gain of new habitat is high (Ketterson & Nolan 1983). The macaws in Belize need fly only a small distance over the Maya Mountain crest and into the eastern low-elevation areas to find polewood, wild annatto, and mo tree at sites like Red Bank.

King (1998a) suggested that macaws in the Chiquibul would be forced to forage elsewhere in January and February because of low amounts of food. My phenology data from the Chiquibul area show times of lowest fruit availability from July through October. The discrepancy may be due to differences in weather or observation methods and sites. In general it is common for fruit production in the dry season to be a limiting factor (Terborgh 1986). I regard a lack of nest and roost cavities, increased territoriality limiting foraging, and a period of less food in the dry season as the major drivers of Scarlet Macaw migration in Belize. An additional factor drawing macaws to low elevations is the availability of superabundant food with little or no competition.

My research showed high food abundance just after the migrants move to either low or high-elevation habitats. I found a significant correlation between the presence of ripe polewood fruit and the number of macaws at low-elevation Red Bank, where there was also abundant wild annatto and the mo tree. At Red Bank, eating was the macaws' primary activity with no observable secondary activity other than resting in the middle of the day's heat. In the midst of this abundant food, there was no observable competition or territorial defense behavior. In 2006, macaws did not come to Red Bank when there was a lack of fruit (Romero 2004).

Migrant Scarlet Macaws leave the high-elevation Chiquibul area just before the beginning of the breeding season, which is also just before the coldest months of the year, January and February. Older adults may be larger and better able to adapt to the cold winter than younger smaller birds according to the “body-size” hypothsis (Ketterson & Nolan 1983). Although Belize is subtropical, cold fronts come from the north – impacting up to 12 days in the month of January (National Meteorological Service 2006), when egg laying may begin in the Chiquibul. These “northers” can bring lows of 5.5° C (Brokaw 1991). My meterological data from 2001-2004 at low-elevation Jaguar Creek, Belize, show that such fronts can drop the minimum daily temperature 5° C in a day (eg. 17.72° to 12.77° Jan. 8-9, 2009), with lower temperatures lingering a few days.

Elevational cooling (approx. 6° C less per 1,000 m gain) (Rich et al. 1992) applied to the roughly 500 m elevation difference between Red Bank and Las Cuevas, means that Las Cuevas is approximately 3°C cooler on average. In the Chiquibul, a cold front would drop the normal low an additional 5° C, and fronts bring winds and wind chill. Such conditions would require macaws to consume more food or decrease their activity to maintain homeostasis. During such a cold front, riverine areas (the Macal and Raspaculo Branch) would receive extra cold, downslope mountain winds at night, making a well-insulated nest cavity, tens of meters above the lowest and coldest air at the river’s surface, highly desirable, especially when incubating eggs.

The “limited foraging” hypothesis emphasizes that inclement weather reduces foraging opportunities so that small-bodied birds needing frequent foraging bouts migrate to lower-elevations (Boyle 2008c, 2011). That hypothesis assumes higher rainfall in higher-elevations, which was not true for the western side of the Chiquibul where all of my high-elevation plots were located. Macaws are also large-bodied frugivores more likely to be able to wait out inclement weather than the small-bodied birds studied by Boyle (2008, 2011), but weather may still have an impact on macaw migration in Belize. Scarlet Macaws used a clay lick in Peru much less in inclement weather (Brightsmith 2004b) and I observed that rain showers stopped all foraging activity at Red Bank. It seems plausible that prolonged rains could limit foraging to a considerable extent and that limited foraging in a colder period of food scarcity might provide incentive to seek food elsewhere.

One last speculative reason why macaws migrate out of the Chiquibul may be that pre-colonial breeding grounds could have included the low-elevation Atlantic pine savannas, making the Chiquibul a second-choice breeding area. Loss of former nesting sites in the low elevations may mean that habitat in the Chiquibul has become crowded with a smaller number of possible territories and nest cavities - effectively limiting the population.

As in annual long-distance migration, weather impacts migrants in Belize. In colder temperatures the Chiquibul may be unattractive or even deadly for young macaws, and for others incapable of the competition required to hold a nest site or roost site. Macaw migrants may be influenced to move up river courses over the Maya Mountain crest and along eastern river courses into the lower-elevations where unused habitat is measurably warmer, free of territorial claims and threats of physical violence, and rich with a superabundance of ripe preferred fruit.

Movements Over the Maya Mountains

Perhaps macaws could fly from the Chiquibul to a low-elevation site like Red Bank and then fly back in a day, but that seems highly unlikely. In general, parrots that make daily trips of 30-40 km are “not unusual” (Collar 1997), and a few parrots, African Grey (*Psittacus erithacus*), Blue-headed (*Pionus menstruus*) and *Eclectus* ssp., make “substantial daily movements between communal roosting areas and feeding places” (Juniper & Parr 1998). Elsewhere, in Guatemala, radio-collared adult Scarlet Macaws took foraging trips of 10-15 km from the nest (Moya & Castillo Villeda 2002); in Costa Rica, radio-collared Scarlet Macaw fledglings flew as far as 15 km a day, gradually making larger and larger movements to forage (Myers & Vaughan 2004). However, just one daily flight from the Macal and Raspaculo Branch confluence to Red Bank and back (straight line flight ≈ 94 km), would be quite energy-intensive. In this scenario breeding males would fly to Red Bank, fill up with food for two adult birds plus any nestlings, and then return, a feat unlikely to leave them enough time or energy to make more than one trip that day. Multiple foraging trips in one day to feed nesting females and nestlings have been noted as the norm in Mexico (Iñigo-Elias 1996; Arroyo 2000), Guatemala (Villeda 2000), and Costa Rica (Vaughan 2002). In Belize, Renton (1998b) noted an average of 3.3 feedings per day by the male for the female on the nest or nestlings. In addition, the macaw is a large bird and “the constraint of reduced climb rate in large birds could be important as they climb to reach their flying altitude or to cross mountain ranges” (Newton 2010). This reduced climb rate would make multiple daily flights over the Maya Mountains energy-intensive and also explain why the macaws prefer to move along rivers, the lowest areas in their mountainous habitat.

In season, flocks of macaws move daily between Red Bank and a likely upstream roosting site approximately four to eight kilometers northwest in the Sapote Creek drainage area or in two similar creeks north of it on either side of Cerro Blanco and Ciudad. These flights of macaws moving up the Swasey branch of the Monkey River could look like dusk flights toward the mountains and Chiquibul to the west, but I saw some macaws in Red Bank at dusk and dawn, so all the macaws in that area do not fly over the Maya Mountains overnight (pers. obs. 2009). Night flight of Scarlet Macaws has been recorded, but is quite rare: Rodas et al. (2001) document one case in Guatemala and there are a few observations in Belize.

In Guatemala, satellite tagging of three breeding adults showed they stayed in the general area, within 25 km, of the nest (Boyd & McNab 2008). To see if breeding macaws in Belize make large movements, in May 2011 satellite tracking collars (Telonics Argos Necklace for Psittacines – TAV-2627) were placed on three breeding female macaws caught at nests with chicks greater than 25 days old along the upper Macal River and a tributary called Blossom Berry Creek, and tracked through December 2011. These three females "continued to return and utilize area around the nest for the entirety of the 8 months" (Britt et al. 2011). With nest exploration and egg-laying in January, the females were in the Chiquibul year-round. Because of the presence of chicks and because macaws are most often found in mated pairs (Collar 1997), they probably had mates with them. This is strong evidence that breeders do not migrate to the low-elevation areas such as Red Bank. Britt et al. (2011) assume that the young fledged and traveled in with their parents, as happens in Guatemala (Moya & Castillo Villeda 2002; Cohouj, pers. comm. 2005) and probably also in Mexico, since Mexican and Guatemalan Scarlet Macaw populations are intermingled (Rodas et al. 2001; Boyd & McNab 2008). Flights with young have also been observed in Honduras (Portillo Reyes et al. 2005a; Portillo Reyes et al. 2005b), and in Costa Rica, where a study found extensive parental feeding for 11 weeks post-fledging (Myers & Vaughan 2004).

What happens with the non-breeders? In December and January, as paired macaws settle into nest territories in the Chiquibul, it would be natural for excluded non-breeders to forage and flock together. Flocks are a common occurrence in migrating birds that are short-distance migrants using widely scattered food resources (Ketterson & Nolan 1983). Flocking assists younger birds to avoid predation and leads them to food resources (Berthold 2001). Young initial migrants would benefit from being taught about new foods from the older birds; polewood is not ripe in January in the Chiquibul, so would be a new food for the young birds in the low-elevation areas. This assistance could be important as parrots are generally neophobic, but in one study social dominance did not influence individual parrots that displayed neophobic behavior (Mettke-Hofmann et al. 2002). Flocking in migrants also assists juveniles to find wintering ranges (Berthold 2001). Older birds may lead the younger birds in migration to the low-elevation areas. In several species, notably cranes and geese, older birds transmit migration route information, as seen in tracking and banding studies, and evidenced by our ability to lead them to new areas (Ellis et al. 2003; Urbanek et al. 2010).

Once in the low elevations, migrant macaws likely have communal roosting sites at large trees; these sites may facilitate foraging communication (Ward & Zahavi 1973; Rabenold 1986; Torney et al. 2011). Communal roosts have not yet been found in Belize (though I suspect one near Red Bank), but do exist in Mexico (Iñigo-Elias 1996; Arroyo 2000), Honduras (Portillo Reyes et al. 2004; Portillo Reyes et al. 2005a), Costa Rica (Vaughan 2002), and Panama (Wetmore 1957; Balaguer 2010).

Migrants “are wanderers because their resources on which they depend are ephemeral” (Rappole 1995). In Belize, migrants in the low-elevation areas move from one locale to another, likely going from one choice foraging site to another. Daily foraging movement at Red Bank was often down the Swasey Branch to the hills behind the village, with a reverse flight late in the afternoon. From the consistent daily numbers I recorded, I surmised that local flocks developed at Red Bank, and at BFREE on the Bladen River. Large flocks seen flying away from Red Bank towards the Cockscomb Basin to the north (Meerman 1999; pers. obs. 2007-2009) could have been moving to another foraging site. In some species, according to Newton (2008), “once individuals have wintered in an area, they return year after year.” This behavior may occur at Red Bank, as there are macaw flocks there every year; perhaps other flocks prefer the BFREE area or the Cockscomb Basin. This preference could influence their movements over the Maya Mountains, so that certain flocks use one pass and others use another pass to go to another area. Another possibility is that all these migrants initially move to Red Bank, and then macaws spread out making local flocks in different areas.

Movements Back to the Chiquibul

Low and incrementally rising numbers of macaw sightings in the Chiquibul from January to March could be due to females not being visible while in the nest cavity (Renton 1998b). Large increases in macaw sightings in the Chiquibul appear linked to March and April movement out of the low-elevation areas and Red Bank. A dramatic jump in sightings in the Chiquibul from April to June would be expected because by then both adults and any fledglings are out of the nest.

Peaking in February at 116 individuals in large flocks at Red Bank, migrant macaw numbers plummeted in low elevations during March; by April I saw no macaws in any of the low-elevation plots, in nearby areas, or in the eastern Maya Mountain foothills. This absence was confirmed in all the other sighting records I collected; villagers in Red Bank see it as an annual natural phenomenon. The exception is a few sightings in the Cockscomb Basin throughout the summer and early fall. By a process of elimination, if macaws are not on the coastal plain farther east, and not in the eastern foothills, they must be in the high slopes of the Maya Mountains or in the Chiquibul. Sighting records at Las Cuevas, and records gathered by FCD rangers during my research, confirm the jump in my macaw sightings in the Chiquibul in April, with more in May and a large peak in June. All these observations suggest return migration to the Chiquibul. What factors could influence these migratory movements?

Scarcity of polewood may be the proximate cause of outmigration in the low-elevation areas and Red Bank area. By mid- April, polewood, the major food at Red Bank, was in low supply and no other super- abundant fruit was available there. In an Amazon study that included experimental harvest of food, Scarlet Macaws were considered “food-sensitive,” with visits to the harvested areas completely ceasing (Moegenburg & Levey 2003); something like that may explain the abrupt departure of macaws from Red Bank. A diet study by Renton (2006) noted that polewood in Red Bank was eaten from March through May, so there may be some annual variation of this important food and in macaw departure.

Abundance of food in the Chiquibul may also draw macaws from the low elevations when polewood is ripe at the higher-elevations; however ripe polewood in high-elevation plots did not show any unique association with rising macaw numbers, possibly because many foods became ripe between March and May. Macaws have been seen eating polewood in the Chiquibul region from March to May (Gentle, pers. comm. 2008; pers. obs. 2009). FAI scores indicate that food is not in short supply when the migrants return to the Chiquibul in March and April, and in May and June the scores peak. For large frugivores in Central America, fruit abundance “could be the proximate factor that initiates migration to the highlands” (Chaves-Campos 2004). In Costa Rica, a study indicated that Scarlet Macaw numbers dramatically peaked in one month due to one abundant food (Penard et al. 2008). Curiously, I found a very large spike in the low-elevation FAI in May caused primarily by a large increase in wild annatto fruit at Red Bank, but no macaws were there.

Unlike long-distance migrants that move back to a breeding area, macaws returning to the Chiquibul are not likely to breed. On average it takes Scarlet Macaws 70 days to go from hatching to fledging (Garcia et al. 2004). If the migrants returned to the Chiquibul to breed in mid-March, we would expect to see new active nests then and fledging by the end of May. The latest recorded nesting activity is from the Macal River (July 25, 2002) where there were fledglings in two nests and a third nest had chicks that were still being fed (Mallory & Matola 2002b). Those could be renesting attempts similar to one in which eggs were in a nest June 24 after a predation event earlier in the season (Britt 2010c). It seems unlikely that there would be two rounds of breeding, one by the competent breeders, and a later one started by returning migrants; satellite tagging showed the first breeders keep and use the nest cavities (Britt et al. 2011).

Migrants returning to the Chiquibul may find territoriality diminished in May and June because breeders are no longer sitting on the nest cavity all day and are foraging in wider circles. With local population numbers at their annual high after fledging there could be an overconcentration of macaws in well-used riverine areas. This might create pressure to forage in even higher-elevation areas following ripening fruit.

Sightings of Scarlet Macaws drop precipitously in all areas of the Chiquibul after May and June, but macaws are also completely absent from Red Bank and all of the lower eastern foothills (with a few exceptions in Cockscomb). I hypothesize that the macaws continue a seasonal elevational migration finding ripe polewood and other fruits on the high western and eastern slopes of the Maya Mountain crest. Polewood and other food trees have been seen on these high ridges (Brokaw 1991; Mallory 1994; Matola & Sho 2002a; Penn et al. 2004); Scarlet Macaws have also been seen there (Russell 1964; Matola & Sho 2002b) and flying high in that direction in May (Mallory 1994). My data show that polewood follows a sequential elevational ripening between the low elevations and the Chiquibul where my plots were, so polewood and other macaw-foods may ripen at even higher-elevations in July, August, or possibly later. Macaws foraging on these remote high areas would not likely be seen by people because there are no habitations between the Macal and Raspaculo Branch and the Maya Mountain crest. Getting to the crest requires an expedition.

Three macaw movement studies have been carried out on or near the Maya Mountain crest between the Chiquibul and Cockscomb. The first indicated numerous flights toward the Maya Mountain crest in May (Mallory 1994); in the next study macaws were seen along the way to the crest and heard flying over in March, and in August there were no sightings along the same route used in March (Mallory & Matola 2002a). The May sightings may have represented high-elevation feeding on the crest, or possibly foraging just on the other side of the divide; low-elevation areas have no macaws in May, except the few in Cockscomb. The March sightings were thought to be movement toward Red Bank; macaws are there in March, but there are few then. Problematic for my August through October high-elevation feeding hypothesis is the August expedition to the crest produced no sightings of macaws at all (Matola & Sho 2002a).

Another explanation of few sightings from August to October is that the macaws are molting then, and may fly less often and only short distances; fewer flights would dramatically decrease sightings. Parrots molt all feathers annually, a process that takes several months and occurs after breeding (Collar 1997). Scarlet Macaw specimens obtained in El Salvador in August and September were in the midst of their annual molt (Dickey & van Rossem 1938). According to Newton (2010), “short-distance migrants molt in summer after breeding”; he describes molt migration as movement to an area where molt occurs. Rappole (1995) noted that during molt, passerines “often move to sites away from the breeding area … and to habitats different from the breeding area.”

A possible complication with my hypothesis of continued elevational migration is that there could be difficulties foraging in the height of the wet season in these high-elevation areas, which are also areas of high rainfall (2540-3048 mm) (Walker 1973). However, wet season also means warmer temperatures, possibly allowing foraging at this higher, and cooler, elevation. In Peru; annual rainfall of 3,236 mm and evenly warm temperatures are the norm for Scarlet Macaws (Brightsmith 2004b).

Summary: Partial, Differential, Facultative, and Elevational Migration

Of the two types of partial migration, “facultative partial migration” best describes macaw movement in Belize, with environmental factors such as seasonally abundant food, seasonal temperature variances, and nest cavity scarcity all becoming incentives for movement. It seems clear the entire population of macaws does not move. According to Newton (2010), “In many partial migrants, migration can be regarded as facultative.” Partial migration is likely driven by seasonal food abundance (Jahn et al. 2010; Sekercioglu 2010) which would make it facultative. Newton (2010) writes “Facultative migrants tend to migrate shorter distances, and to travel by day”; this is seen in Belize’s migrant macaws. One definition of facultative migration includes the possibility that environmental conditions could be favorable and the species not migrate (Terrill & Able 1988); very good environmental conditions in the Chiquibul could have been a factor in the year when macaws did not come to Red Bank, but lack of polewood at Red Bank was regarded as the primary factor in their absence (Romero 2004).

The migrant macaws of Belize might be considered genetically-programmed or obligate, partial migrants because of their consistent annual movement. This movement is a differential migration of birds that do not breed, and hence likely not a separate group with different genes. The migrants are also unlikely to be a separate population since all known breeding takes place in the same area and when the migrants are away. However, two distinct haplotypes of macaws exist within the Belize population (Feria & de los Monteros 2007b; Schmidt & Amato 2008, 2009), leaving open the possibility that there may have been obligate resident and obligate migrant populations in the past. How might this partial, facultative, elevational migration have developed?

One theory of how migration develops is that the current breeding range “is the original year-round home of a population, while the wintering range is the secondary home, visited to enhance survival through the most difficult season” (Newton 2010). This scenario sounds very much like what occurs in Belize, with the Chiquibul the current and ancestral breeding site. In other seasonal migrations in Mexico, Nicaragua, and Honduras, breeding takes place in the low elevations with movement to higher areas after breeding. Another migration development theory is that “the present wintering range is the original year-round home, while the breeding range is the secondary home, visited to enhance reproductive success” (Newton 2010). Such a situation could have developed in Belize if the macaws lost their normal breeding ground to logging and retreated to the Chiquibul area. Most of Belize’s human population now lives in or near pine savanna on the coastal plain, where there are now few or no large pines left after centuries of logging and frequent hurricanes. Logging may have eliminated breeding in another area with pine savanna, the Mountain Pine Ridge (MPR). Macaws have not been there since 1985 (Kainer 1990), although some sightings still occur along the Macal River which borders it and Britt et al. (2011) document one flight within the MPR. Removal of large pines would have forced this subpopulation to breed elsewhere, perhaps in the Chiquibul, where they may have gone annually in search of seasonally abundant food. In support of my speculation is the fact that that migrants now fly when breeding begins in the Chiquibul; this behavior could be left over from flights to their lower-elevation breeding grounds.

CONCLUSIONS: PROPOSALS FOR RESEARCH AND CONSERVATION

Research

Tagging of macaws would clearly assist with determining seasonality and direction of movement. Satellite tagging of breeding macaws has been done once in Belize with good results (Britt et al. 2011). One way to test my facultative partial migration hypothesis would be to weigh captured macaws and take tissue samples to determine sex and haplotype. One of two previously reported haplotypes (Schmidt & Amato 2008, 2009) may be more migratory. So far all captures of Scarlet Macaws in Belize have been at the nest, but breeding macaws stay in the Chiquibul and do not migrate to the low-elevation areas (Britt et al. 2011). Captures of macaws at Red Bank in February might yield sex and age information via blood and feather samples to verify that these birds are the young and older non-breeders.

After capture, some method of marking and tracking movements would be desirable. No effective bands have been developed yet that are highly visible and survive the macaw's beak; a number of marking methods were tried with mixed success (Hilburn & Higgins 2000). Radio and satellite tags do survive the beak and also provide location and activity information. Britt (2011) used satellite tags successfully in the Chiquibul; standard radio tags would not work well in this rugged area due to the necessity of line-of-sight transmission for accurate radio-tag locations. Radio tags could be used to monitor local movement between a suspected roost site in Sapote Creek and Red Bank, and also possibly between Red Bank and other eastern foothill sites. Birds radio-tagged in Red Bank could also be detected by radio signals from manned or automatic antennae at previously identified passes in the Maya Mountains.

Still somewhat enigmatic is where Scarlet Macaws are from August to October. Macaw sightings in those months have historically been zero in low-elevation areas and low in the Chiquibul. Consistent point counts throughout the year should be conducted in both low- and high-elevation areas. The FCD guardhouse at the Caracol Junction is a good point count site with trained personnel and an almost constant presence. Red Bank Village or Sho's Fine Vista in the hills near Red Bank would both be good sites to monitor presence. To see if macaws move to still higher-elevations, and thus escape notice, would require a series of expeditions with extended stays on the crest of the Maya Mountains between Cockscomb and the Chiquibul area. Rappelling from a helicopter and return via foot might be the most efficient methods of transport. Expeditions to Doyle's Delight, Belize's highest peak, used a helicopter landing on a helipad cut into the forest (Teul 2009). Observations of movement over the Maya Mountains could be made from the passes; in March they might show the movement of low-elevation macaws to the Chiquibul. Observations of migration between the low- and high-elevations could also be done from within valleys below those passes.

There are other questions related to movements. For example, why would Chiquibul River macaws migrate all the way to Red Bank? As the macaw flies, it is about 45 km from the Chiquibul River to the southernmost of the three passes described. A formidable massif including Doyle's Delight lies between the Chiquibul River and low-elevation areas to the east. Might these southern-most macaws follow the Chiquibul River into Guatemala instead? Other movement-related questions entail determining if macaws go to Red Bank first and then spread out to form local flocks, and determining how much movement there is between local large flocks of macaws in the low-elevation areas.

Finding all, or many, nests along a river would enhance management activities. Mapping of known and potential nest sites would generate data on number of nests, nest territories, and nest spacing to see if cavities are limited. At the same time, it would be useful to obtain dbh measurements of nest trees and core samples of quamwood trees; many tropical trees have no annual rings, but quamwood does have them (Marcati et al. 2008). These data would be useful for predicting whether an area has potential nests by looking at the area's tree composition, height, and dbh. Determining natural nest territory spacing would allow placement of any artificial nests to avoid competition with natural nests already in use. Mapped nests could be closed or guarded if threatened by *xateros,* and potential nest cavities near live nests could be closed to prevent predators from nesting nearby.

Agonistic behavior in the Chiquibul during the breeding season could also be studied to see if territorial defense increases when breeding season starts, a possible cause for migration by non-breeders. Few reports of territorial defense displays like the one I describe are in print and none discuss territory size, which may impact management decisions and artificial nest box programs for Scarlet Macaws.

Lookout towers could also be created; in Guatemala, this is a preferred method of determining where to look for nests (Garcia et al. 2004). Finding nests away from the rivers is slow work: two years of hard work in Guatemala resulted in discovering 24 new nests in the Parque Nacional Laguna del Tigre area (Garcia et al. 2004). Aerial flights (Britt 2010a) could be used to find bright yellow quamwood trees, possible nest sites, during their flowering period. Another research possibility is analysis of spectral reflection from satellite imagery which has been used both to identify tree species important to unidentified macaws and determine the seasonal phenology of the trees (Papes 2009).

My phenology work in the Chiquibul did not account for foods eaten in the riparian areas where macaws spend significant amounts of time. Phenology work within the Macal and Raspaculo Branch could determine food availability and seasonality, and if there are keystone fruits. For example, figs are a known macaw-food in Belize and *Ficus insipida, F. glabrata*, and *F. guajavoides* have been identified along the Macal and Raspaculo (Brokaw 1991; Minty 2001; Mallory & Matola 2002b; Urban et al. 2006); we do not know if figs in these riverine areas have year-round fruit or how much of it the macaws eat.

To determine if lack of nest cavities is a major limiting factor, another attempt could be made to place nests in the appropriate spots. Artificial nests could be made from quamwood and with two levels that allow young to escape to the bottom level if a predator appears at the top-level entrance (Garcia et al. 2008); such nests are used more if wood chips are placed in the boxes (Boyd & McNab 2008). In Guatemala, artificial nest boxes made of cantemo wood (*Acacia angustissima* or *A. glomerosa*), similar in many ways to quamwood, greatly reduced the time and effort used in placing nests (Garcia et al. 2006). Quamwood could be cut and the boxes made far from the placement area and flown in via helicopter. The other transport option is canoe transport, a very tedious choice due to shallow water in the Macal and Raspaculo and weight of the artificial nests. The current plastic-tube artificial nests were very difficult to get to sites (Tunich-Nan Consultants & Engineering 2005a, b). Natural and potential nests must be mapped before artificial nests are placed to avoid creating unnecessary competition between macaws.

Might Scarlet Macaws breed in sites like Red Bank? I have shown that it is possible they did in the past and there may be enough food; if artificial nests were introduced macaws might nest in them, although they might be used only for roosting. If the macaws at Red Bank breed, they would be paired birds capable of reproduction, so not too young or too old, but also not sufficiently competitive to obtain food or a nest site in the Chiquibul breeding grounds. The artificial nests could be made from native pine in imitation of possible historical nests, or of quamwood. An organization out of North Carolina and Mango Creek/Independence, Belize, planned to erect artificial nests around Red Bank in January 2005 with foreign volunteers (Medicine Trail Research Center 2005), but did not do so.

I believe that Red Bank habitat will support nestlings. On the edge of pine savanna, it is a habitat that supports nesting in eastern Honduras and likely eastern Nicaragua. There pine (*Pinus caribea* var. *hondurensis*), which is the same pine as in Belize's savanna, is used for nesting with an average entrance height of 24.7 m in trees of 0.8 dbh (N = 13) (Portillo Reyes et al. 2010b). Good sites for artificial nests include along the Swasey River upstream from Red Bank, at Sapote Creek, at Macaw Valley, and possibly in the creek that flows from the hills behind Red Bank. At least one artificial nest should be placed so that tourists can see it when they climb to Sho's Fine Vista to observe feeding macaws. Several of these artificial nests may need nest guarding; success depends on the people of Red Bank and nearby San Pablo.

Conservation Activities

Aside from the elevational movements I have described, there is another seasonal pattern of movement in Belize closely linked to the reproductive cycle of macaws: the movement of nestling poachers to Belize. Poaching is the most pressing anthropogenic problem for Scarlet Macaws in Belize, as it is for most Scarlet Macaws in Central America and Mexico. In Belize, what can be done in the sort-term is to prevent or reduce access to nesting areas, make nest-tree climbing unpleasant or dangerous, prevent use of nest trees that are likely to be poached (i.e., close the cavity) (Vaughan et al. 2003b; Briceno-Linares et al. 2011), guard nest trees when likely to be poached (Vaughan et al. 2003b; Boyd & McNab 2008; Briceno-Linares et al. 2011), collect nestlings before poachers do and release nestlings later (Briceno-Linares et al. 2011), and effectively prosecute poachers. Long-term solutions to poaching will require environmental education in both Belize and Guatemala, strengthening of enforcement related to natural resource conservation, and economic development that raises the standard of living for Guatemalans so that they will not come to Belize and poach these beautiful birds. More on this subject is in Appendix L.

Looking to the future, even if poaching is reduced or eliminated, the need for habitat will remain. My analysis of current macaw sightings in Belize and Belize's *A Protected Area System Assessment and Analysis* (Meerman 2005b; Meerman & Wilson 2005) indicate that most of the known Scarlet Macaw habitat is within protected areas, but as Belize's human population rapidly expands, some habitat loss continues even in protected areas. A prime example is the Chalillo Dam hydroelectric project constructed in the Chiquibul National Park. Studies were conducted of Scarlet Macaws within the projected impoundment area and serious concerns were raised (Minty 2001), but the dam was still built despite fierce environmental activist opposition (Trivedi 2003; Barcott 2008; pers. obs. 2003). Vaca Dam, downstream from the Mollejon and Chalillo Dams, became operational in January or February 2010 (Britt 2010a; Casallas 2010). With these three dams Belize can supply about 70% of its domestic electricity needs, the rest coming from Mexico (Marion 2009). It is estimated that 90% of the Scarlet Macaws in Belize, despite being mostly in protected areas, still face threats from legal mining and logging, and from rampant poaching (Britt et al. 2011). Many of the protected areas are not adequately patrolled because of lack of funds. More on this subject is in Appendix L.

Meerman (1999) proposed creating a new protected area that took in the Red Bank hills and connected them with unprotected government lands adjacent to Cockscomb Wildlife Sanctuary to the north. This included the unprotected hills west of the Swasey branch of the Monkey River, just outside the boundaries of the Maya Mountain Forest Reserve (Fig. 25). Meerman's plan wisely excludes flat land in agricultural use, or of possible use as agricultural land, and preserves connectivity between the Red Bank hills and the much larger protected areas of the Maya Mountain Forest Reserve and Cockscomb Basin Wildlife Sanctuary.

My proposal is to extend the Maya Mountain Forest Reserve and create a Red Bank Preserve, thus joining the Red Bank area to the Maya Mountain Forest Reserve (MMFR) and providing protection to a critical riparian area (Fig. 26). The MMFR should be extended to the hills adjacent to San Pablo Village, as close as will be tolerated. In the past, these hills have had numerous macaws feeding on them, but feeding has diminished as villagers have converted much of the hillsides to crops. If the hills immediately north of San Pablo could not be protected, then a line should be drawn excluding the south-facing slopes and starting at the base of the north-facing slopes. As a pioneer species, polewood may regrow naturally when fields are abandoned, but replanting would be better. In a January 2012 conversation with a Belize Audubon board member I was informed of possible plans to engage Mennonite farmers near Red Bank in a project to produce Scarlet Macaw food trees for replanting in the Red Bank area.

Protection of the area around the Swasey branch of the Monkey River is important because the river functions as a transit route and is used as foraging habitat, so I propose that the MMFR extend over the Swasey branch of the Monkey Tail River and 250 meters on its eastern side to protect the riparian zone. This extension of the MMFR would also provide protection to the Sapote Creek area that I highly suspect to be a roosting site for the majority of the macaws that frequent Red Bank. My proposal ignores the northern hills past the ones visible from Red Bank, since I saw practically no key food plants on them and noted they are between two agricultural areas, the fields north of Red Bank and west of Maya Mopan.

This extension of the MMFR would mostly avoid current agricultural areas and there is no reason to curtail agricultural usage of any land within the proposed boundaries, provided farmers do not expand into uncut land. These inholdings may cause management problems, but eliminating the inholdings would greatly lessen local support for the protected area. In addition, a separate protected area, east of the river and perhaps called the Red Bank Preserve, should encompass the Macaw Hill and Guesthouse Ridge areas, with different protections afforded to each. Macaw Hill should be a “no hunting” and “no logging” area, while the Guesthouse Ridge area, closed to hunting, would be open for sustainable use, particularly for wood products, although excluding the primary food trees of polewood, wild annatto, and the mo tree. Planting these macaw-food trees on Guesthouse Ridge could repair some of the damage created by wood cutting; certainly trees of other valuable species could be planted as well.

Administration of the additional land added to the Maya Mountains Forest Reserve would be retained by the government, but I see two different possibilities for the Red Bank Preserve, which would be wholly on government land. The first is for Red Bank Village to declare unilaterally that Macaw Hill and Guesthouse Ridge are protected areas and to administer them as such. The village, with a vested interest in the natural resources of the hills, including the macaws, would be able to enforce any prohibitions decided on, and could gather people for resource improvement activities such as tree planting. Although the government owns the land, it does nothing to manage it. If the village proclaimed this area a wildlife sanctuary, I see no reason why government officials would object, other than on grounds of not following procedure. These objections might easily be overlooked in view of the benefits to the macaws and the village. This route to protection acknowledges that the village will be looking after the area whether it is officially or unofficially a wildlife sanctuary, and would be a decision made by and for the village. Another possibility, which may be assisted by the first, but need not be preceded by it, is to seek official proclamation of the hills as a wildlife sanctuary. This route to protection would likely take several years and would require an expensive physical survey to delineate protected lands. In this scenario the government of Belize and the village would co-manage the area. Numerous protected areas in Belize are co-managed by non-governmental organizations and the government, allowing both legal protection and local input into management.

Aside from elimination of poaching by *xateros*, education is certainly the long-term key to the Scarlet Macaw’s survival in Belize and elsewhere. Educational projects or products focused on Scarlet Macaws have been created in Mexico (Cantu et al. 2009; Mendez 2009; Sanchez & Mendez 2009) and in Guatemala (Durán de Benítez & León 2004; Tut et al. 2005). I was able to see WCS-Guatemala environmental education efforts in villages in 2007 and I understand they continue. In Honduras, proposed education programs have not yet begun (Portillo Reyes et al. 2005a). In Nicaragua, there are no specific educational programs, but Scarlet Macaws are included in national programs to reduce the illegal commerce of wildlife (Lezama, pers. comm. 2010). In Costa Rica, several educational projects have focused on Scarlet Macaws (Araujo 1998; Zoo Conservation Outreach Group 1999; Vaughan 2002; Vaughan et al. 2003a; Dear et al. 2005a; Dear et al. 2005b), and LAPPA continues to conduct environmental education in the Carara National Park area (The Association for the Protection of Psittacines (LAPPA) 2010).

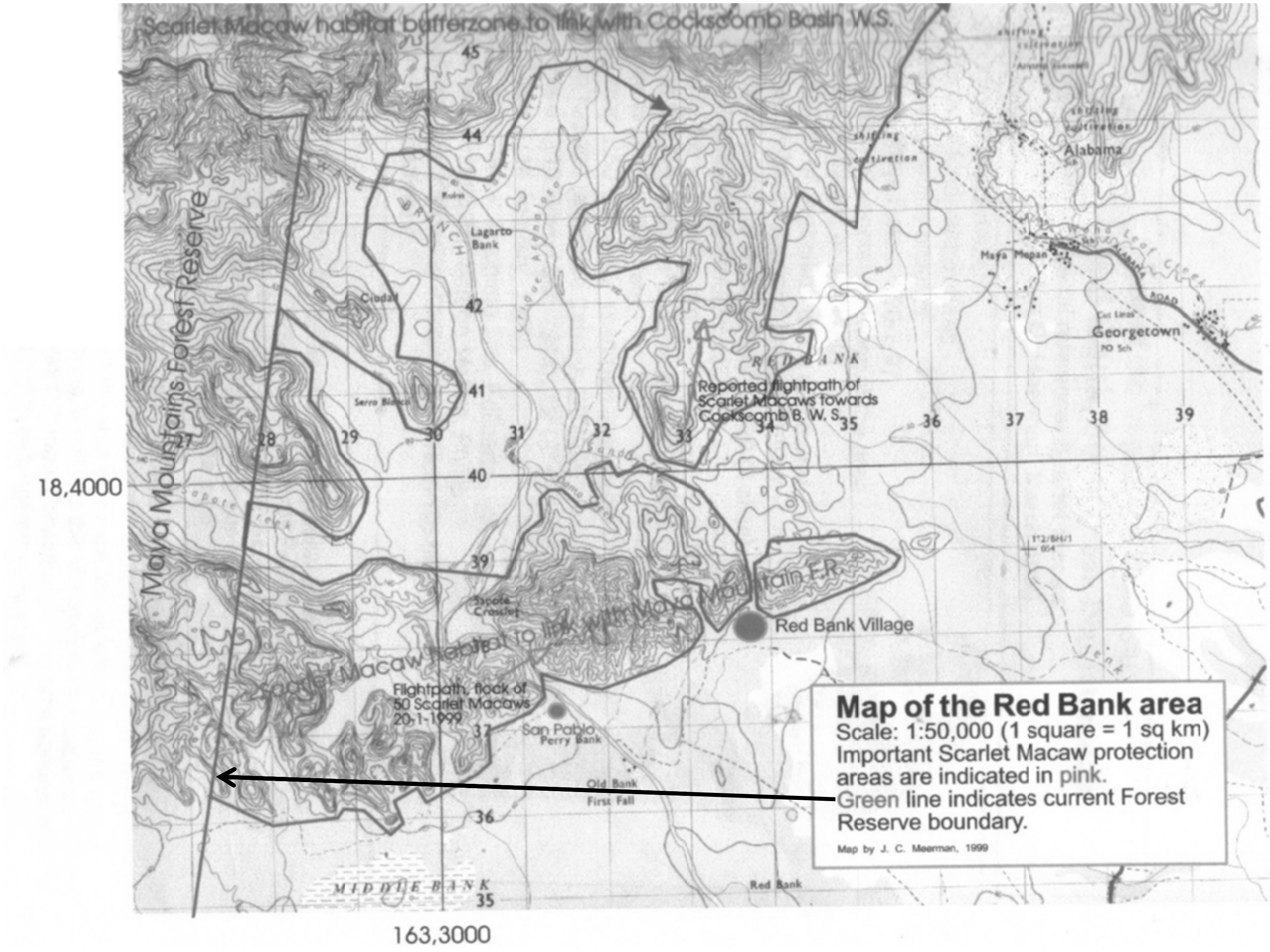


Figure 25. Meerman's proposed protected area, Red Bank, Belize. Map from Meerman (1999).

Within Belize, the Belize Zoo has been at the forefront of environmental education efforts for Scarlet Macaws (Loro Parque Fundación 2000, 2001; Poot 2001), producing a poster (The Belize Zoo 2001) and children's books (Matola 1988, 2000), as well as bringing many programs to schools.

After a widely publicized poaching incident at Red Bank (Belize Audubon Society 1997), Programme for Belize started environmental education and an ecotourism project in Red Bank Village

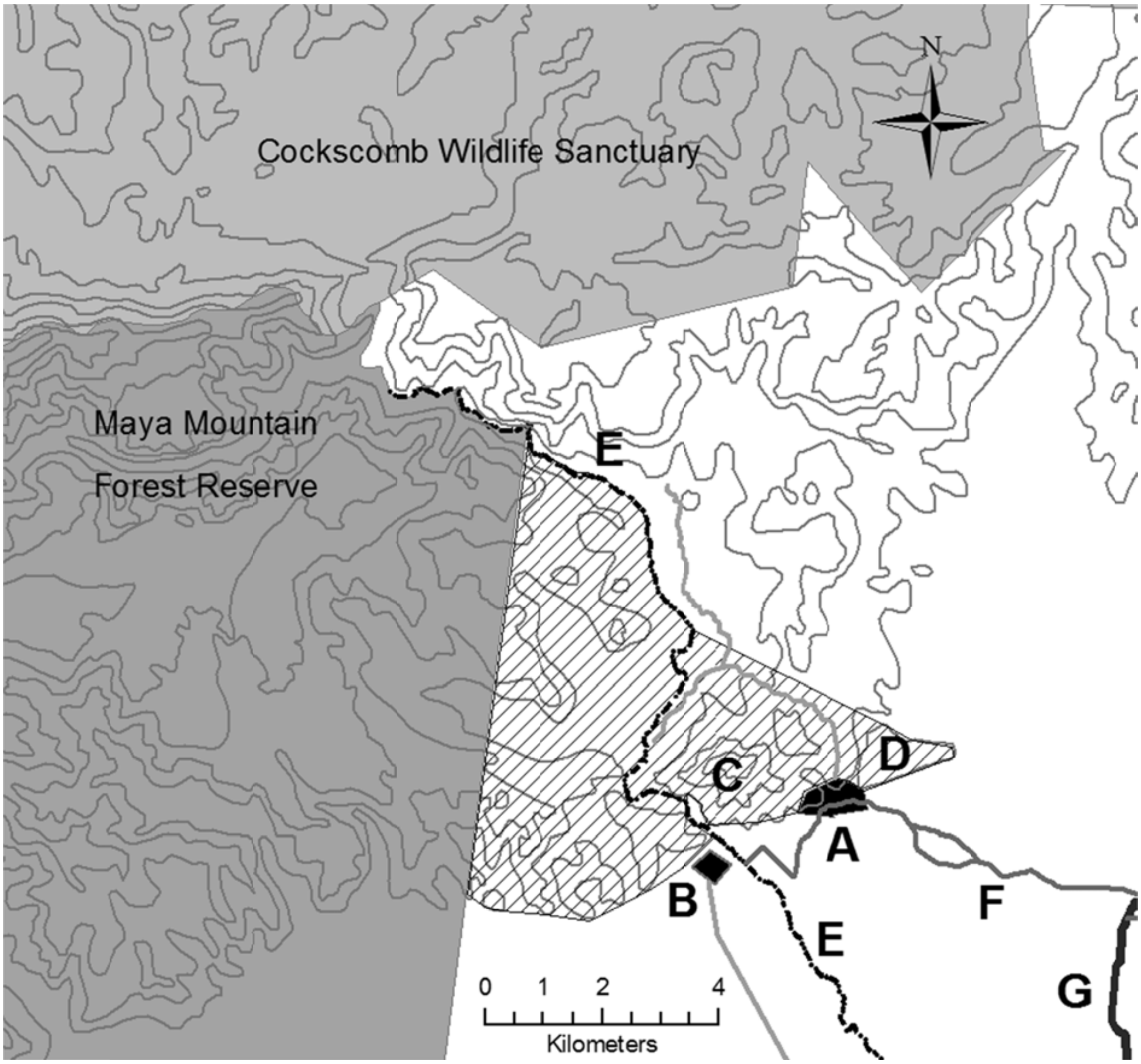


Figure 26. A proposed preserve in Red Bank, Belize, and extension of the Maya Mountain Forest Reserve. This map shows existing (solid gray), and proposed protected area (hatched), Red Bank Village (A), San Pablo Village (B), Macaw Hill (C), Guesthouse Ridge (D), Swasey branch of the Monkey River and boundary between Cayo and Toledo Districts (E), the road to Red Bank (F), and the Southern Highway (G). GIS files used from Meerman and Sabido (2001) and revised 2004; map MMc.

focused on protection of Scarlet Macaws (Romero 2004). That program is now dormant. Recently FCD looked for an umbrella species on which to base conservation education and social marketing (Rare Conservation 2010). After surveying people in villages near the Maya Mountains, FCD selected the Scarlet Macaw as a representative for their efforts. FCD puts on many school and community programs with a human-sized Scarlet Macaw mascot figure that talks and sings. FCD has also produced t-shirts, posters, and bumper stickers with Scarlet Macaws prominently affixed. More on the role of education in conserving Belize's macaws is in Appendix L.

My minimum population count of 117 individual Scarlet Macaws in Belize and estimate of approximately 200 individual Scarlet Macaws appears reasonable given previous estimates, but that makes them one of the smallest subpopulations within Central America and Mexico, with only Panama's subpopulation smaller - unless one counts El Salvador, where they were extirpated (Thurber 1978; Thurber et al. 1987; Komar & Dominguez 2001; Bjork 2008; Bjork & Komar 2008).

More scientific research into the natural history and ecology of Scarlet Macaws in Belize, including studies of diet and seasonal and elevational movements, is certainly needed, as are effective anti-poaching actions and the new preserve around Red Bank Village. Without education these efforts will not be enough. After15 years of environmental education experience in the U.S., I regret not being able to do more to help in this way, but hope to do so in the future. The 200 or so Scarlet Macaws, as they move from Red Bank Village to the Chiquibul and back, will eventually move from an endangered status to an extirpated status, unless educated citizens of Belize act. A phrase often heard in Belize is "at the end of the day." At the end of the day and through the next few decades, it is the people of Belize who will decide the fate of this beautiful bird. I pray they succeed.

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APPENDICES

APPENDIX A

SOURCES OF SCARLET MACAW SIGHTINGS IN MEXICO AND CENTRAL AMERICA

Although one can easily find parrots and macaws in Central American tourist-promotion literature, limited records of observations appear in the scientific literature. No comprehensive source of information on Scarlet Macaw sightings in Central America exists. Apart from general field guides, both current and historical national-range maps are rare, an exception being one for Costa Rica (Conservation Breeding Specialist Group - IUCN 2006).

For each country, I conducted a literature search for historical information on range and observations from colonial times to the present. I built a database of 3,314 sighting records with source, location, and other information for all Central American countries and Mexico. Aside from my work in Belize, I made research trips to Guatemala and Costa Rica, adding more records. I searched for sighting records in journals and websites, and made use of Request for Information emails to the NEOORN – listserv (Remsen 2009) and Bird Chat listservs (Otte et al. 2009), as well as the Bird Chat and Bird Trip Archives (Otte et al. 2009) and the Avian Knowledge Network (Avian Knowledge Network 2011).

I collected museum-specimen and locality-record data from records held in the following institutions (accessed through the ORNIS data portal (http://ornisnet.org) up to 19 July 2010): American Museum of Natural History (AMNH); Academy of Natural Sciences (ANSP); Borror Laboratory of Bioacoustics (BLB); California Academy of Sciences (CAS); Carnegie Museum of Natural History (CMNH); Delaware Museum of Natural History (DMNH); Denver Museum of Natural Science (DMNS); Field Museum of Natural History (FMNH); Harvard University Ornithology Collection (MCZ); Kansas State University Natural History Museum (KSUNHM); Los Angeles County Museum of Natural History (LACM); Louisiana State University Museum of Zoology (LSUMZ); Royal Ontario Museum (ROM); UCLA Dickey (UCDickey); Museum of Vertebrate Zoology at University of California, Berkeley (MVZ); University of Colorado Museum of Natural History (UCM or CUMNH); University of Michigan Museum of Zoology (UMMZ); Western Foundation of Vertebrate Zoology (WFVZ); and Yale Peabody Museum (YPM).

Other institutions supplying data were: Cleveland Museum of Natural History (CM) via Wiedenfeld, David A. (1994); United States National Museum (USNM); British Museum of Natural History (BMNH); the Natural History Museum of Denmark; University of Copenhagen (NHMD); the Cornell Lab of

Ornithology’s eBird (Cornell Laboratory of Ornithology 2010); and Avian Knowledge Network (Avian Knowledge Network 2011).

Using sighting data from all sources I mapped historic and current distribution of Scarlet Macaws in Central America and Mexico. To construct my distribution maps, I used publications and associated GIS files from Mapa de Ecosistemas de Centroamerica (World Bank and CCAD 2001); administrative boundaries within countries (Hijmans et al. 2011); and a world base map (Olson et al. 2001).

APPENDIX B

SOURCES OF OTHER MACAW SIGHTINGS IN BELIZE

I compiled Scarlet Macaw records other than my own from numerous sources. Records with the largest number of sightings were 454 (Bol & King 1996; King 1998a), 13 (Kamstra 1987, 1996), 67 (Mallory 1991, 1994; Mallory & Matola 2002a), 17 (Matola & Sho 1998; Matola & Sho 2002a), and 148 (Minty 2001). Lesser numbers were 6 (Colston 1995), 3 (McRae 2000), and 7 (Kainer 1990). Renton's macaw research in Belize (Renton 1998a, 1998b, 2006) is summarized in several reports but few sightings with numbers or locations can be deduced from them. The Natural History Museum in London has eight records and the Louisiana State University Museum of Zoology has one record and the only known specimens from Belize other than those alive in the Belize Zoo.

Las Cuevas Research Station (LCRS) had 644 records; the Belize Foundation for Research and Environmental Education (BFREE), 67 records; Chiquibul Base operated by Friends for Conservation and Development (FCD), 179 records; Bladen Nature Reserve (BNR), 16 records; Cockscomb Basin Wildlife Sanctuary (CBWS), 13 records; and a logbook I set up at Sho's Fine Vista in Red Bank had 49 records. The Biodiversity & Environmental Resource Data System of Belize (BERDS) (Meerman 2010) provided a few records as well. Searching internet-posted birder trip records, Cornell Laboratory of Ornithology's E-Bird, and the NEOORN list-serv provided a few sightings. No records were used from the Avian Knowledge Network (Avian Knowledge Network 2011) except for use in mapping distribution.

Many individuals were helpful in reporting presence sightings, most notably Jeronimo Sho and family of Red Bank, 55 sightings; Nicodemas and Celia Bol of LCRS, 102 sightings (many more in the LCRS logbook); FCD Rangers, 208 (many more in their logbook); British soldiers, 24; Dr. Bruce Miller, 52; BFREE staff, 30; Zoe Goodwin, 12; Charles Britt, 9. A few sightings, but mostly absence data, were noted by jaguar researchers Ashley Bies, Miranda Davis, and Claudia Wultsch. Absence data were also collected from literature (Brokaw et al. 1987; Parker et al. 1993; Teul 2009).

APPENDIX C

PROTECTED AREAS WITHIN THE STUDY AREA

Type	Management	Co-management Partner	Km^2
Bladen Nature Reserve	Forest Department	Bladen Management Committee	403.37
Chiquibul Forest Reserve	Forest Department	None	598.22
Chiquibul National Park	Forest Department	Friends for Conservation and Development	1068.39
Cockscomb Basin Wildlife Sanctuary	Forest Department	Belize Audubon Society	494.77
Maya Mountain Forest Reserve	Forest Department	None	168.88
Mayflower Bocawina National Park	Forest Department	Friends of Mayflower Bocawina	31.78
Mountain Pine Ridge Forest Reserve	Forest Department	None	430.40
Nojkaaxmeen Eligio Panti National Park	Forest Department	Tanah - Nojkaaxmeen Eliji	51.31
Sibun Forest Reserve	Forest Department	None	328.48
Sittee Forest Reserve	Forest Department	None	373.59
Vaca Forest Reserve	Forest Department	None	141.18
Victoria Peak Natural Monument	Forest Department	None	19.59
BFREE Private Reserve	Belize Foundation for Research and Environmental Education	None	5.72
Vaca Forest Reserve	Forest Department	None	141.18
Caracol Archeological Reserve	National Institute of Culture and History	None	103.40

Information from Meerman (2008b).

APPENDIX D

PHENOLOGY PLOT DETAILS

EASTERN PHENOLOGY PLOTS IN BELIZE

Base	Plot Name	Elev. (M)	Ecosystem	UNESCO Description
Belize Foundation for Research and Environmental Education	Maya Mountain Forest Reserve	55	lowland broad-leaved wet forest	IA1a(1)(b)P corresponding to tropical evergreen broad-leaved lowland forest on poor or sandy soils (Meerman & Sabido 2001).
	Bladen Nature Reserve	73	lowland broad-leaved wet forest	IA1f(2)(a)K corresponding to tropical evergreen broad-leaved wet forest (Meerman & Sabido 2001).
Red Bank Village	Macaw Valley	233	lowland broad-leaved moist forest	IA2a(1)(a)-ST corresponding to tropical evergreen seasonal broad-leaved lowland hill forest, and Simarouba-Terminalia variant (Meerman & Sabido 2001)
	Guesthouse Ridge	123	lowland broad-leaved moist forest	IA2a(1)(a)-ST corresponding to tropical evergreen seasonal broad-leaved lowland hill forest, and Simarouba-Terminalia variant (Meerman & Sabido 2001)
Cockscomb Wildlife Sanctuary	Mexican Branch Trail	80	Shrubland	IIIB1b(f)H corresponding to deciduous broad-leaved lowland riparian shrubland in hills (Meerman & Sabido 2001).
	Snook Eddy	4	lowland broad-leaved moist forest	IA2a(1)(b)S corresponding to tropical evergreen seasonal broad-leaved lowland forest on poor or sandy soils (Meerman & Sabido 2001).

WESTERN PHENOLOGY PLOTS: Chiquibul Area, Cayo, Belize.

Base	Plot Name	Elev. (M)	Ecosystem	UNESCO Description
Friends For Conservation and Development Guardhouse	Guacamallo Bridge Road	404	lowland broad-leaved moist forest	IA2a(1)(a)K-s corresponding to Tropical evergreen seasonal broad-leaved lowland hill forest on steep karstic terrain (Meerman & Sabido 2001)
	Caracol Road	442	lowland broad-leaved moist forest	IA2b(1)K-s corresponding to tropical evergreen seasonal broad-leaved lowland hill forest on steep karstic terrain and IA2b(1)K-s tropical evergreen seasonal broad-leaved submontane forest on steep karstic hills (Meerman & Sabido 2001).
FCD Guardhouse or **Las Cuevas Research Station**	Cubetas	643	submontane broad-leaved moist forest	IA2b(1)K-r corresponding to tropical evergreen seasonal broad-leaved submontane forest on rolling karstic hills (Meerman & Sabido 2001).
	San Pastor	597	submontane broad-leaved moist forest	IA2b(1)-VT corresponding to tropical evergreen seasonal broad-leaved submontane forest: Virola-Terminalia variant (Meerman & Sabido 2001).
Las Cuevas Research Station	Monkey Tail Trail	554	submontane broad-leaved moist forest	IA2b(1)-VT corresponding to tropical evergreen seasonal broad-leaved submontane forest: Virola-Terminalia variant (Meerman & Sabido 2001).
	Las Cuevas	570	submontane broad-leaved moist forest	IA2b(1)K-r corresponding to tropical evergreen seasonal broad-leaved submontane forest on rolling karstic hills (Meerman & Sabido 2001).

WESTERN PHENOLOGY PLOT: Guacamallo Bridge Road polewood plot, Cayo, Belize.

Base	Plot Name	Elev. (M)	Ecosystem	UNESCO Description
Friends For Conservation and Development Guardhouse	Guacamallo Bridge Road Polewood	404	lowland broad-leaved moist forest	IA2a(1)(a)K-s corresponding to Tropical evergreen seasonal broad-leaved lowland hill forest on steep karstic terrain (Meerman & Sabido 2001).

PHENOLOGY PLOT CREATION AND SAMPLING SCHEDULE.

Phenology and Bird Count Plot **Plot Name (Creation Date)**	2008 **Jul.**	**Aug.**	**Sep.**	**Oct.**	**Nov.**	**Dec.**	2009 **Jan.**	**Feb.**	**Mar.**	**Apr.**	**May.**	**Jun.**	**Total**
Bladen (May 08)	F	S	S	S	S	S	S	S	S	S	S	S	**11**
Caracol Road (Aug 08)	NC	S	S	S	S	S	S	S	S	S	S	S	**11**
Cubetas (Apr 08)	S	S	S	R	S	S	S	S	S	S	S	S	**11**
Guacamallo Bridge Road (Jul 08)	S	S	S	S	S	S	S	S	S	S	S	S	**12**
Guac. Bridge Rd. - Polewood (Apr 08)	S	NS	S	S	S	S	S	S	S	S	S	S	**11**
Guesthouse Ridge (Feb 08)	S	S	S	S	S	S	S	S	S	S	S	S	**12**
Las Cuevas (Aug 08)	NC	S	S	R	S	S	S	S	S	S	S	S	**10**
Macaw Valley (Feb 08)	S	S	S	S	S	S	S	S	S	S	S	S	**12**
Mexican Branch Trail (Jun 08)	S	S	F	F	S	S	S	S	S	S	S	S	**10**
Maya Mountains F. R. (Jun 08)	F	S	R	S	S	S	S	S	S	S	S	S	**10**
Monkey Tail Trail (Apr 08)	S	S	S	R	S	S	S	S	S	S	S	S	**11**
San Pastor (Apr 08)	S	S	S	R	S	S	S	S	S	S	S	S	**11**
Snook Eddy Trail (Jun 08)	S	S	F	F	S	S	S	S	S	S	S	S	**10**
Monthly Total	**9**	**12**	**10**	**7**	**13**	**13**	**13**	**13**	**13**	**13**	**13**	**13**	

Number of Plots Sampled Per Month

NC = not Created
F = no access due to flood
R = no access due to impassable road
NS = not sampled
S = sampled

PHENOLOGY PLOT COORDINATES

Coordinates are based off of NAD 1927 UTM 16N readings and digitized with a conversion program (Dutch 2009). Not all locations had coordinates due to poor GPS reception.

Plot Points	Lat.	Long.
Bladen Nature Reserve plot: 0 M	16.555289	-88.718146
Bladen Nature Reserve plot: 100 M	16.556209	-88.718369
Bladen Nature Reserve plot: 200 M	16.556912	-88.718675
Bladen Nature Reserve plot: 300 M	16.557765	-88.719245
Bladen Nature Reserve plot: 400 M	16.558683	-88.719769
Bladen Nature Reserve plot: 500 M	16.558070	-88.720616
Caracol Road plot 0 M	16.844648	-89.046166
Caracol Road plot 200 M	16.844710	-89.048156
Cubetas plot: 0 M	16.783903	-89.015445
Cubetas plot: 100 M	16.783486	-89.014728
Cubetas plot: 200 M	16.783369	-89.013695
Cubetas plot: 300 M	16.783142	-89.012980
Cubetas plot: 400 M	16.782917	-89.011918
Cubetas plot: 500 M	16.782743	-89.011212
Guacamallo Bridge Road plot (On Road)	16.856048	-89.037328
Guacamallo Bridge Road plot 0 M	16.856128	-89.037508
Guacamallo Bridge Road plot 100 M	16.856700	-89.038077
Guacamallo Bridge Road plot 400 M	16.858888	-89.039789
Guacamallo Bridge Road plot 500 M	16.859523	-89.040434
Guacamallo Bridge Road Polewood plot End (291 m long)	16.856602	-89.037043
Guacamallo Bridge Road Polewood plot Start (291 m long)	16.854143	-89.038077
Guesthouse Ridge plot: 0 M	16.622423	-88.557763
Guesthouse Ridge plot: 100 M	16.622765	-88.556791
Guesthouse Ridge plot: 200 M	16.623433	-88.556824
Guesthouse Ridge plot: 300 M	16.623557	-88.555907
Guesthouse Ridge plot: 400 M	16.624239	-88.555462
Guesthouse Ridge plot: 500 M	16.624580	-88.554584
Las Cuevas plot 0 M	16.726304	-88.989476
Las Cuevas plot 100 M	16.726493	-88.988596
Las Cuevas plot 200 M	16.726673	-88.987801
Las Cuevas plot 400 M	16.727243	-88.985791
Las Cuevas plot 500 M	16.727722	-88.984896
Macaw Valley plot: 0 M	16.620119	-88.583998
Macaw Valley plot: 100 M	16.621214	-88.582620
Macaw Valley plot: 200 M	16.621130	-88.581757
Macaw Valley plot: 300 M	16.620791	-88.581136
Macaw Valley plot: 400 M	16.621238	-88.580549
Macaw Valley plot: 500 M	16.621939	-88.579983
Maya Mountain For. Res. plot: 0 M	16.553946	-88.697971
Maya Mountain For. Res. plot: 100 M	16.554685	-88.698268
Maya Mountain For. Res. plot: 200 M	16.555577	-88.698520
Maya Mountain For. Res. plot: 300 M	16.556514	-88.698893
Maya Mountain For. Res. plot: 400 M	16.557106	-88.699451

Maya Mountain For. Res. plot: 500 M	16.557654	-88.699840
Mexican Branch Trail plot: 0 M	16.772973	-88.528516
Mexican Branch Trail plot: 100 M	16.773507	-88.529618
Mexican Branch Trail plot: 300 M	16.774698	-88.531015
Mexican Branch Trail plot: 400 M	16.775127	-88.531741
Mexican Branch Trail plot: 500 M	16.775727	-88.532412
Monkey Tail Trail plot: 0 M	16.739166	-88.945490
Monkey Tail Trail plot: 100 M	16.739938	-88.945948
Monkey Tail Trail plot: 200 M	16.740684	-88.946405
Monkey Tail Trail plot: 300 M	16.741265	-88.947040
Monkey Tail Trail plot: 400 M	16.741321	-88.947903
Monkey Tail Trail plot: 500 M	16.741566	-88.948684
San Pastor plot: 0 M	16.711360	-88.984774
San Pastor plot: 100 M	16.710658	-88.985432
San Pastor plot: 200 M	16.709775	-88.986135
San Pastor plot: 300 M	16.708964	-88.986802
San Pastor plot: 400 M	16.708462	-88.987397
San Pastor plot: 500 M	16.707951	-88.987888
Snook Eddy Trail plot: 0 M	16.774437	-88.462646
Snook Eddy Trail plot: 100 M	16.774950	-88.473006
Snook Eddy Trail plot: 200 M	16.774730	-88.464646
Snook Eddy Trail plot: 300 M	16.774452	-88.465554
Snook Eddy Trail plot: 400 M	16.774147	-88.466509
Snook Eddy Trail plot: 500 M	16.773779	-88.467378

APPENDIX E

TAGGED TREE SPECIES LIST

Because I initially tagged all unknown trees as well as known Scarlet Macaw food plants, this list of tagged trees includes both categories of trees.

- **Anacardiaceae**
  - **Astronium**
    - graveolens
  - **Metopium**
    - brownei
  - **Mosquitoxylum**
    - jamaicense
  - **Spondias**
    - mombin
    - purpurea
    - radlkoferi
    - sp.
- **Annonaceae**
  - **Annona**
    - reticulata
    - scleroderma
  - **Cymbopetalum**
    - mayanum
  - **Oxandra**
    - belizensis
  - **Sapranthus**
    - campechianus
  - **Xylopia**
    - frutescens
- **Apocynaceae**
  - **Allamanda**
    - cathartica
  - **Aspidosperma**
    - cruentum
    - megalocarpon
    - spruceanum
  - **Mortoniella**
    - pittieri
  - **Stemmadenia**
    - donnell-smithii
  - **Tabernaemontana**
    - amygdalifolia?
    - arborea
- **Araliaceae**
  - **Dendropanax**
    - arboreus
  - **Schefflera**
    - morototoni
- **Arecaceae**
  - **Attalea**
    - cohune
  - **Sabal**
    - mauritiiformis
  - **Unknown**
    - sp.
- **Bombacaceae**
  - **Bernoullia**
    - flammea
  - **Ceiba**
    - pentandra
  - **Ochroma**
    - pyramidale
- **Boraginaceae**
  - **Cordia**
    - alliodora
    - bicolor
    - stellifera?
- **Bromeliaceae**
  - **Unknown**
    - sp.
- **Burseraceae**
  - **Bursera**
    - simaruba
  - **Protium**
    - confusum
    - copal
    - copal var. glabrum
- **Capparaceae**
  - **Forchhammeria**
    - trifoliata
- **Caricaceae**
  - **Jacaratia**
    - dolichaula
- **Cecropiaceae**
  - **Cecropia**
    - obtusifolia
    - peltata
  - **Pourouma**
    - bicolor
    - bicolor scobina
- **Chrysobalanaceae**
  - **Hirtella**
    - guatemalensis
  - **Licania**
    - hypoleuca
    - platypus
    - platypus?
- **Clusiaceae**
  - **Calophyllum**
    - brasiliense
    - brasiliense rekoi
    - brasiliense var. rekoi
  - **Garcinia**
    - intermedia
  - **Symphonia**
    - globulifera
- **Cochlospermaceae**
  - **Cochlospermum**
    - vitifolium
- **Combretaceae**
  - **Combretum**
    - fruticosum
  - **Terminalia**
    - amazonia

Cucurbitaceae

- **Cionosicys**
  - excisus
  - macranthus
  - sp.

Elaeocarpaceae

- **Sloanea**
  - tuerckheimii

Euphorbiaceae

- **Alchornea**
  - latifolia
- **Cnidoscolus**
  - aconitifolius
  - aconitifolius [chayamansa]
  - multilobus
  - multilobus multilobus
  - souzae
  - sp.
  - tubulosus
- **Croton**
  - schiedeanus
  - sp.
- **Pera**
  - arborea
  - barbellata
- **Pleradenophora**
  - longicuspis

Fabaceae

- **Acacia**
  - angustissima
  - angustissima var. angustissima
  - collinsii
  - cookii
  - cornigera
  - dolichostachya
  - farnesiana var. farnesiana
  - gentlei
  - globulifera
  - glomerosa
  - polyphylla
  - sp.
- **Andira**
  - inermis
- **Ascosmium**
  - panamense
- **Cojoba**
  - arborea
  - arborea arborea
  - graciliflora
- **Dalbergia**
  - stevensonii
- **Dialium**
  - guianense
- **Gliricidia**
  - sepium
- **Inga**
  - affinis
  - belizensis
  - cocleensis
  - cocleensis cocleensis
  - davidsei
  - densiflora
  - edulis
  - jinicuil
  - multijuga
  - nobilis quaternata
  - oerstediana
  - pavoniana
  - pinetorum
  - punctata
  - quaternata
  - quaternata?
  - sapindoides
  - sp.
  - thibaudiana
  - vera
  - vera spuria
  - vera vera
- **Lecointea**
  - amazonica
- **Lonchocarpus**
  - rugosus
  - sp.
- **Myroxylon**
  - balsamum
- **Ormosia**
  - velutina
- **Pithecellobium**
  - arboreum
- **Platymiscium**
  - dimorphandrum
- **Pterocarpus**
  - officinalis
  - rohrii
  - sp.
- **Schizolobium**
  - parahyba
- **Swartzia**
  - cubensis
  - simplex
  - sp.
- **Vatairea**
  - lundellii

Flacourtiaceae

- **Casearia**
  - arguta?
  - sylvestris
- **Zuelania**
  - guidonia

Lacistemataceae

- **Lacistema**
  - aggregatum

Lamiaceae

- **Vitex**
  - gaumeri

Lauraceae

- **Licaria**
  - peckii
- **Nectandra**
  - belizensis
  - coriacea
  - cuspidata
  - hihua
  - longicaudata
  - lundellii

- nitida
  Lauraceae Cont.
  Nectandra Cont.
  salicifolia
- sp.
  turbacensis
- **Ocotea**
  - cernua
- **Unknown**
  - sp.

Loganiaceae

- **Strychnos**
  - peckii

Malpighiaceae

- **Byrsonima**
  - crassifolia

Melastomataceae

- **Miconia**
  - affinis elata
- **Mouriri**
  - exilis
  - myrtilloides
- **Unknown**
  - sp.

Meliaceae

- **Cedrela**
  - odorata
- **Guara**
  - glabra
- **Guarea**
  - grandifolia
  - sp.
- **Swietenia**
  - macrophylla
- **Trichilia**
  - erythocarpa or moshata
  - minutiflora?
  - pallida
  - sp.

Moraceae

- **Brosimum**
  - alicastrum
  - alicastrum alicastrum
- **Castilla**
  - elastica
  - elastica elastica
- **Ficus**
  - americana
  - apollinaris
  - aurea
  - citrifolia
  - colubrinae
  - costaricana
  - crassiuscula
  - donnell-smithii
  - glabrata
  - guajavoides
  - insipida
  - maxima
  - nymphaeifolia
  - obtusifolia
  - ovalis
  - paraensis
  - pertusa
  - popenoei
  - schippii
  - sp.
  - trigonata
  - turrialbana
  - yoponensis
- **Pseudolmedia**
  - spuria
- **Trophis**
  - racemosa

Myristicaceae

- **Compsoneura**
  - mexicana
- **Virola**
  - koschnyi

Myrtaceae

- **Pimenta**
  - dioica
- **Plinia**
  - peroblata
- **Unknown**
  - sp.

Olacaceae

- **Heisteria**
  - media

Polygonaceae

- **Coccoloba**
  - belizensis
  - swartzii

Rhizophoraceae

- **Cassipourea**
  - elliptica
  - guianensis

Rubiaceae

- **Alseis**
  - yucatanensis
- **Exostema**
  - mexicana
- **Guettarda**
  - combsii
- **Psychotria**
  - chiapensis
- **Simira**
  - salvadorensis
- **Unknown**
  - sp.

Rutaceae

- **Zanthoxylum**
  - acuminatum
    acuminatum
    juniperinum
  - belizense
  - caribaeum
  - ekmanii
  - gentlei
  - juniperinum
  - panamense
  - petenense
  - riedelianum
  - riedelianum kellermanii
  - sp.

Sapindaceae

- **Blomia**
  - prisca

Cupania
belizensis

Sapindaceae Cont.
Matayba
sp.
Paullina
sp.
Sapindus
saponaria
Sapotaceae
Manilkara
chicle
sp.
staminodella
zapota
Pouteria
amygdalina
amygdaloides
campechiana
durlandii
durlandii durlandii
izabalensis
reticulata
sapota
Sideroxylon
stevensonii
Sideroxylon
capiri tempisque

Simaroubaceae
Simarouba
glauca
Sterculiaceae
Byttneria
catalpifolia
catalpifolia catalpifolia
Guazuma
ulmifolia
ulmifolia var. tomentella
Tiliaceae
Heliocarpus
mexicana
Luehea
seemannii
speciosa
Trichospermum
grewiifolium
Violaceae
Rinorea
sp.
Vochysiaceae
Vochysia
hondurensis
hondurensis var. parvifolia

APPENDIX F

NON-PLOT PHENOLOGY RECORD SOURCES

Sources of non-plot phenology records came from the online database *BERDS* with 1457 records (Meerman 2010); the online database *Tropicos,* 1,103 (Tropicos.org 2010); Dr. Steven Brewer, 158 (all on two of the phenology plots); and my own records, 621 outside my established phenology plots. Smaller numbers of records came from the Belize Foundation for Research and Environmental Education (BFREE) Logbook, 13; Bol & King (1996), 9; the Nicodemas Bol family from LCRS, 30; Forest Department Herbarium, 36; FCD Rangers, 11; Las Cuevas Research Station (LCRS) Logbook, 15; Matola & Sho (2002a),11; Minty (2001), 29; Royal Botanical Gardens at Kew, 8; Renton (1998a, 1998b), 40; Field Museum (Chicago), 1; Jan Meerman, 6 (in addition to BERDS data). These records, in combination with my plot records, were used to create a food plant list and phenology charts, and determine food availability.

APPENDIX G

COMPLETE BIRD LIST

This list in AOU order (50^{th} version) includes all birds identified by sight or vocalization by me during my research in Belize. These records came from work on the research plots and many other sites. Details are preserved in a database.

	Common Name	**Genus species**	**Family**
1	Great Tinamou	*Tinamus major*	Tinamidae
2	Little Tinamou	*Crypturellus soui*	Tinamidae
3	Blue-winged Teal	*Anas discors*	Anatidae
4	Plain Chachalaca	*Ortalis vetula*	Cracidae
5	Crested Guan	*Penelope purpurascens*	Cracidae
6	Great Curassow	*Crax rubra*	Cracidae
7	Black-throated Bobwhite	*Colinus nigrogularis*	Odontophoridae
8	Singing Quail	*Dactylortyx thoracicus*	Odontophoridae
9	Spotted Wood-quail	*Odontophorus guttatus*	Odontophoridae
10	Ocellated Turkey	*Meleagris ocellata*	Phasianidae
11	Neotropic Cormorant	*Phalacrocorax brasilianus*	Phalacrocoracidae
12	Anhinga	*Anhinga anhinga*	Anhingidae
13	Magnificent Frigatebird	*Fregata magnificens*	Fregatidae
14	Bare-throated Tiger-heron	*Tigrisoma mexicanum*	Ardeidae
15	Great Blue Heron	*Ardea herodias*	Ardeidae
16	Great Egret	*Ardea alba*	Ardeidae
17	Snowy Egret	*Egretta thula*	Ardeidae
18	Little Blue Heron	*Egretta caerulea*	Ardeidae
19	Reddish Egret	*Egretta rufescens*	Ardeidae
20	Cattle Egret	*Bubulcus ibis*	Ardeidae
21	Green Heron	*Butorides virescens*	Ardeidae
22	Yellow-crowned Night-heron	*Nyctanassa violaceus*	Ardeidae
23	Boat-billed Heron	*Cochlearius cochlearius*	Ardeidae
24	White Ibis	*Eudocimus albus*	Threskiornithidae
25	Jabiru	*Jabiru mycteria*	Ciconiidae
26	Black Vulture	*Coragyps atratus*	Cathartidae
27	Turkey Vulture	*Cathartes aura*	Cathartidae
28	King Vulture	*Sarcoramphus papa*	Cathartidae
29	Osprey	*Pandion haliaetus*	Accipitridae
30	Gray-headed Kite	*Leptodon cayanensis*	Accipitridae
31	Swallow-tailed Kite	*Elanoides forficatus*	Accipitridae
32	Plumbeous Kite	*Ictinia plumbea*	Accipitridae
33	White Hawk	*Leucopternis albicollis*	Accipitridae
34	Common Black-hawk	*Buteogallus anthracinus*	Accipitridae
35	Great Black-hawk	*Buteogallus urubitinga*	Accipitridae
36	Solitary Eagle	*Harpyhaliaetus solitarius*	Accipitridae
37	Roadside Hawk	*Buteo magnirostris*	Accipitridae
38	Gray Hawk	*Asturina nitida*	Accipitridae
39	White-tailed Hawk	*Buteo albicaudatus*	Accipitridae
40	Zone-tailed Hawk	*Buteo albonotatus*	Accipitridae
41	Red-tailed hawk	*Buteo jamaicensis*	Accipitridae
42	Black Hawk-eagle	*Spizaetus tyrannus*	Accipitridae

43	Ornate Hawk-eagle	*Spizaetus ornatus*	Accipitridae
44	Black-and-white Hawk-eagle	*Spizastur melanoleucus*	Accipitridae
45	Barred Forest-Falcon	*Micrastur ruficollis*	Accipitridae
46	Collared Forest-Falcon	*Micrastur semitorquatus*	Accipitridae
47	Laughing Falcon	*Herpetotheres cachinnans*	Accipitridae
48	Ruddy Crake	*Laterallus ruber*	Rallidae
49	Rufous-necked Wood-rail	*Aramides axillaris*	Rallidae
50	Gray-necked Wood-rail	*Aramides cajanea*	Rallidae
51	Limpkin	*Aramus guarauna*	Aramidae
52	Spotted Sandpiper	*Actitis macularia*	Scolopacidae
53	Solitary Sandpiper	*Tringa solitaria*	Scolopacidae
54	Rock Dove	*Columba livia*	Columbidae
55	Pale-vented Pigeon	*Columba cayennensis*	Columbidae
56	Scaled Pigeon	*Columba speciosa*	Columbidae
57	Short-billed Pigeon	*Columba nigrirostris*	Columbidae
58	Ruddy Ground-Dove	*Columbina talpacoti*	Columbidae
59	Blue Ground-Dove	*Claravis pretiosa*	Columbidae
60	Gray-headed Dove	*Leptotila plumbeiceps*	Columbidae
61	Gray-chested Dove	*Leptotila cassini*	Columbidae
62	Ruddy Quail-Dove	*Geotrygon montana*	Columbidae
63	Olive-throated Parakeet	*Aratinga nana*	Psittacidae
64	Scarlet Macaw	*Ara macao cyanoptera*	Psittacidae
65	Brown-hooded Parrot	*Pionopsitta haematotis*	Psittacidae
66	White-crowned Parrot	*Pionus senilis*	Psittacidae
67	White-fronted Parrot	*Amazona albifrons*	Psittacidae
68	Red-lored Parrot	*Amazona autumnalis*	Psittacidae
69	Mealy Parrot	*Amazona farinosa*	Psittacidae
70	Squirrel Cuckoo	*Piaya cayana*	Cuculidae
71	Striped Cuckoo	*Tapera naevia*	Cuculidae
72	Groove-billed Ani	*Crotophaga sulcirostris*	Cuculidae
73	Common Nighthawk	*Chordeiles minor*	Caprimulgidae
74	Common Pauraque	*Nyctidromus albicollis*	Caprimulgidae
75	Whip-poor-will	*Caprimulgus vociferus*	Caprimulgidae
76	White-collared Swift	*Streptoprocne zonaris*	Apodidae
77	Vaux's Swift	*Chaetura vauxi*	Apodidae
78	Long-billed Hermit	*Phaethornis superciliosus*	Trochilidae
79	Stripe-throated Hermit	*Phaethornis longuemareus*	Trochilidae
80	Wedge-tailed Sabrewing	*Campylopterus curvipennis*	Trochilidae
81	White-necked Jacobin	*Florisuga mellivora*	Trochilidae
82	Violet-crowned Woodnymph	*Thalurania colombica*	Trochilidae
83	White-bellied Emerald	*Amazilia candida*	Trochilidae
84	Rufous-tailed Hummingbird	*Amazilia tzacatl*	Trochilidae
85	Ruby-throated Hummingbird	*Archilochus colubris*	Trochilidae
86	Slaty-tailed Trogon	*Trogon Massena*	Trogonidae
87	Black-headed Trogon	*Trogon melanocephalus*	Trogonidae
88	Violaceous Trogon	*Trogon violaceus*	Trogonidae
89	Collared Trogon	*Trogon collaris*	Trogonidae
90	Blue-crowned Motmot	*Momotus momota*	Momotidae
91	Ringed Kingfisher	*Ceryle torquata*	Alcedinidae
92	Belted Kingfisher	*Ceryle alcyon*	Alcedinidae

93	Amazon Kingfisher	*Chloroceryle amazona*	Alcedinidae
94	Green Kingfisher	*Chloroceryle americana*	Alcedinidae
95	American Pygmy Kingfisher	*Chloroceryle aenea*	Alcedinidae
96	White-whiskered Puffbird	*Notharchus hyperrhynchos*	Bucconidae
97	Rufous-tailed Jacamar	*Galbula ruficauda*	Galbulidae
98	Collared Aracari	*Pteroglossus torquatus*	Ramphastidae
99	Keel-billed Toucan	*Ramphastos sulfuratus*	Ramphastidae
100	Acorn Woodpecker	*Melanerpes formicivorus*	Picidae
101	Black-cheeked Woodpecker	*Melanerpes pucherani*	Picidae
102	Golden-fronted Woodpecker	*Melanerpes aurifrons*	Picidae
103	Smoky-brown Woodpecker	*Veniliornis fumigatus*	Picidae
104	Golden-olive Woodpecker	*Piculus rubiginosus*	Picidae
105	Northern Flicker	*Colaptes auratus*	Picidae
106	Lineated Woodpecker	*Dryocopus lineatus*	Picidae
107	Pale-billed Woodpecker	*Campephilus guatemalensis*	Picidae
108	Rufous-breasted Spinetail	*Synallaxis erythrothorax*	Furnariidae
109	Buff-throated Foliage-gleaner	*Automolus ochrolaemus*	Furnariidae
110	Plain Xenops	*Xenops minutus*	Furnariidae
111	Tawny-winged Woodcreeper	*Dendrocincla anabatina*	Dendrocolaptidae
112	Ruddy Woodcreeper	*Dendrocincla homochroa*	Dendrocolaptidae
113	Olivaceous Woodcreeper	*Sittasomus griseicapillus*	Dendrocolaptidae
114	Wedge-billed Woodcreeper	*Glyphorhynchus spirurus*	Dendrocolaptidae
115	Northern Barred-Woodcreeper	*Dendrocolaptes sanctithomae*	Dendrocolaptidae
116	Ivory-billed Woodcreeper	*Xiphorhynchus flavigaster*	Dendrocolaptidae
117	Streak-headed Woodcreeper	*Lepidocolaptes souleyetii*	Dendrocolaptidae
118	Barred Antshrike	*Thamnophilus doliatus*	Thamnophilidae
119	Dot-winged Antwren	*Microrhopias quixensis*	Thamnophilidae
120	Black-faced Antthrush	*Formicarius analis*	Formicariidae
121	Yellow-bellied Elaenia	*Elaenia flavogaster*	Tyrannidae
122	Ochre-bellied Flycatcher	*Mionectes oleagineus*	Tyrannidae
123	Northern Bentbill	*Oncostoma cinereigulare*	Tyrannidae
124	Slate-headed Tody-Flycatcher	*Poecilotriccus sylvia*	Tyrannidae
125	Common Tody-Flycatcher	*Todirostrum cinereum*	Tyrannidae
126	Stub-tailed Spadebill	*Platyrinchus cancrominus*	Tyrannidae
127	Royal Flycatcher	*Onychorhynchus coronatus*	Tyrannidae
128	Ruddy-tailed Flycatcher	*Terenotriccus erythrurus*	Tyrannidae
129	Sulphur-rumped Flycatcher	*Myiobius sulphureipygius*	Tyrannidae
130	Olive-sided Flycatcher	*Contopus cooperi*	Tyrannidae
131	Tropical Pewee	*Contopus cinereus*	Tyrannidae
132	Yellow-bellied Flycatcher	*Empidonax flaviventris*	Tyrannidae
133	Black Phoebe	*Sayornis nigricans*	Tyrannidae
134	Vermilion Flycatcher	*Pyrocephalus rubinus*	Tyrannidae
135	Bright-rumped Attila	*Attila spadiceus*	Tyrannidae
136	Rufous Mourner	*Rhytipterna holerythra*	Tyrannidae
137	Dusky-capped Flycatcher	*Myiarchus tuberculifer*	Tyrannidae
138	Great Kiskadee	*Pitangus sulphuratus*	Tyrannidae
139	Boat-billed Flycatcher	*Megarynchus pitangua*	Tyrannidae
140	Social Flycatcher	*Myiozetetes similis*	Tyrannidae
141	Streaked Flycatcher	*Myiodynastes maculatus*	Tyrannidae
142	Sulphur-bellied Flycatcher	*Myiodynastes luteiventris*	Tyrannidae

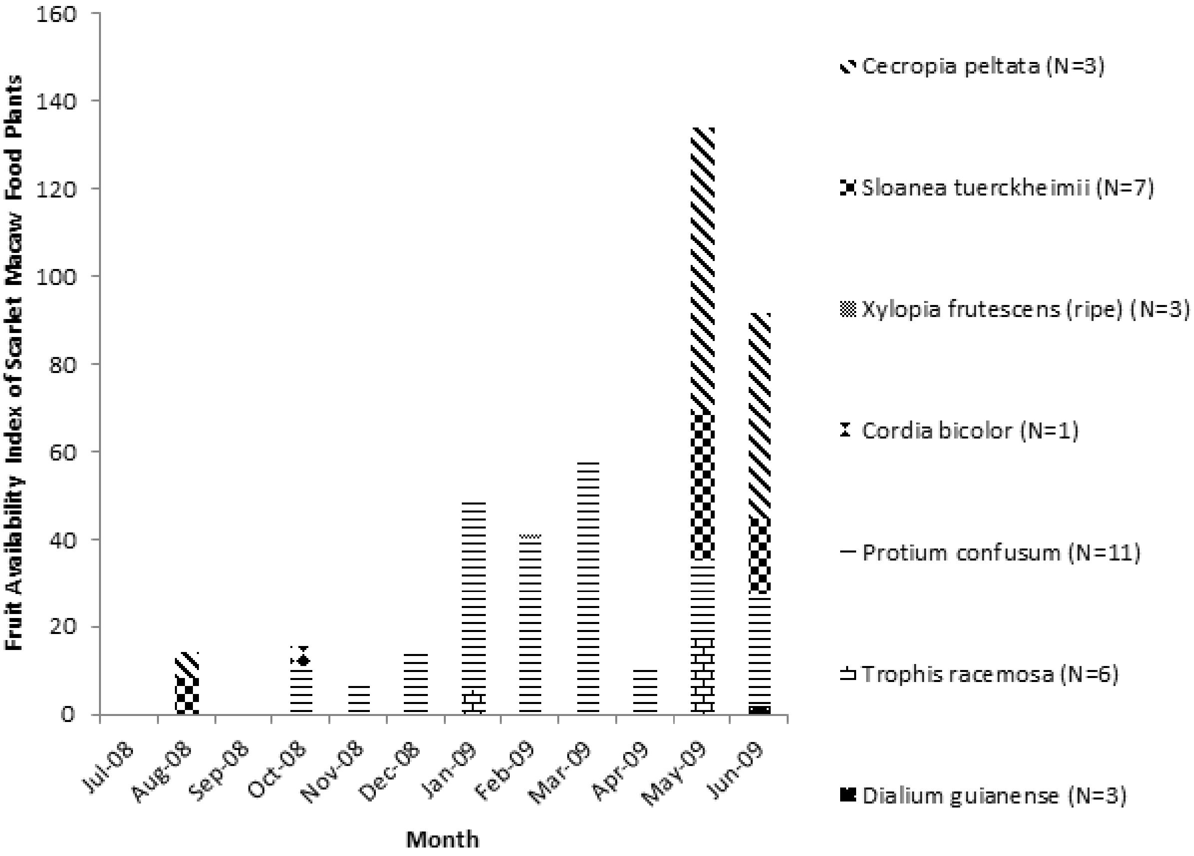
143	Tropical Kingbird	*Tyrannus melancholicus*	Tyrannidae
144	Eastern Kingbird	*Tyrannus tyrannus*	Tyrannidae
145	Fork-tailed Flycatcher	*Tyrannus savanna*	Tyrannidae
146	Thrush-like Schiffornis	*Schiffornis turdinus*	Tyrannidae
147	Rufous Piha	*Lipaugus unirufus*	Tyrannidae
148	Cinnamon Becard	*Pachyramphus cinnamomeus*	Tyrannidae
149	Masked Tityra	*Tityra semifasciata*	Tyrannidae
150	White-collared Manakin	*Manacus candei*	Pipridae
151	Red-capped Manakin	*Pipra mentalis*	Pipridae
152	White-eyed Vireo	*Vireo griseus*	Vireonidae
153	Red-eyed Vireo	*Vireo olivaceus*	Vireonidae
154	Yellow-green Vireo	*Vireo flavoviridis*	Vireonidae
155	Lesser Greenlet	*Hylophilus decurtatus*	Vireonidae
156	Green Shrike-Vireo	*Vireolanius pulchellus*	Vireonidae
157	Brown Jay	*Cyanocorax morio*	Corvidae
158	Mangrove Swallow	*Tachycineta albilinea*	Hirundinidae
159	N. Rough-winged Swallow	*Stelgidopteryx serripennis*	Hirundinidae
160	Bank Swallow	*Riparia riparia*	Hirundinidae
161	Barn Swallow	*Hirundo rustica*	Hirundinidae
162	Band-backed Wren	*Campylorhynchus zonatus*	Troglodytidae
163	Spot-breasted Wren	*Thryothorus maculipectus*	Troglodytidae
164	House Wren	*Troglodytes aedon*	Troglodytidae
165	White-breasted Wood-Wren	*Henicorhina leucosticta*	Troglodytidae
166	Long-billed Gnatwren	*Ramphocaenus melanurus*	Sylviidae
167	Blue-gray Gnatcatcher	*Polioptila caerulea*	Sylviidae
168	Tropical Gnatcatcher	*Polioptila plumbea*	Sylviidae
169	Slate-colored Solitaire	*Myadestes unicolor*	Turdidae
170	Wood Thrush	*Catharus mustelinus*	Turdidae
171	Clay-colored Thrush	*Turdus grayi*	Turdidae
172	White-throated Thrush	*Turdus assimilis*	Turdidae
173	Gray Catbird	*Dumetella carolinensis*	Mimidae
174	Tropical Mockingbird	*Mimus gilvus*	Mimidae
175	Blue-winged Warbler	*Vermivora pinus*	Parulidae
176	Golden-winged Warbler	*Vermivora chrysoptera*	Parulidae
177	Yellow Warbler	*Dendroica petechial*	Parulidae
178	Magnolia Warbler	*Dendroica magnolia*	Parulidae
179	Black-throated Green Warbler	*Dendroica virens*	Parulidae
180	Yellow-throated Warbler	*Dendroica dominica*	Parulidae
181	Black-and-white Warbler	*Mniotilta varia*	Parulidae
182	American Redstart	*Setophaga ruticilla*	Parulidae
183	Prothonotary Warbler	*Protonotaria citrea*	Parulidae
184	Ovenbird	*Seiurus aurocapillus*	Parulidae
185	Northern Waterthrush	*Seiurus noveboracensis*	Parulidae
186	Louisiana Waterthrush	*Seiurus motacilla*	Parulidae
187	Kentucky Warbler	*Oporornis formosus*	Parulidae
188	Common Yellowthroat	*Geothlypis trichas*	Parulidae
189	Gray-crowned Yellowthroat	*Geothlypis poliocephala*	Parulidae
190	Hooded Warbler	*Wilsonia citrine*	Parulidae
191	Golden-crowned Warbler	*Basileuterus culicivorus*	Parulidae
192	Rufous-capped Warbler	*Basileuterus rufifrons*	Parulidae

193	Yellow-breasted Chat	*Icteria virens*	Parulidae
194	Gray-headed Tanager	*Eucometis penicillata*	Thraupidae
195	Black-throated Shrike-Tanager	*Lanio aurantius*	Thraupidae
196	Crimson-collared Tanager	*Ramphocelus sanguinolentus*	Thraupidae
197	Passerini's Tanager	*Ramphocelus passerinii*	Thraupidae
198	Blue-gray Tanager	*Thraupis episcopus*	Thraupidae
199	Yellow-winged Tanager	*Thraupis abbas*	Thraupidae
200	Golden-hooded Tanager	*Tangara larvata*	Thraupidae
201	Green Honeycreeper	*Chlorophanes spiza*	Thraupidae
202	Red-legged Honeycreeper	*Cyanerpes cyaneus*	Thraupidae
203	Grayish Saltator	*Saltator coerulescens*	Thraupidae
204	Buff-throated Saltator	*Saltator maximus*	Thraupidae
205	Black-headed Saltator	*Saltator atriceps*	Thraupidae
206	Blue-black Grassquit	*Volatinia jacarina*	Emberizidae
207	Variable Seedeater	*Sporophila americana*	Emberizidae
208	White-collared Seedeater	*Sporophila torqueola*	Emberizidae
209	Thick-billed Seed-Finch	*Oryzoborus funereus*	Emberizidae
210	Yellow-faced Grassquit	*Tiaris olivacea*	Emberizidae
211	Orange-billed Sparrow	*Arremon aurantiirostris*	Emberizidae
212	Green-backed Sparrow	*Arremonops chloronotus*	Emberizidae
213	Hepatic Tanager	*Piranga flava*	Cardinalidae
214	Summer Tanager	*Piranga rubra*	Cardinalidae
215	Red-crowned Ant-Tanager	*Habia rubica*	Cardinalidae
216	Red-throated Ant-Tanager	*Habia fuscicauda*	Cardinalidae
217	Black-faced Grosbeak	*Caryothraustes poliogaster*	Cardinalidae
218	Rose-breasted Grosbeak	*Pheucticus ludovicianus*	Cardinalidae
219	Gray-throated Chat	*Granatellus sallaei*	Cardinalidae
220	Blue-black Grosbeak	*Cyanocompsa cyanoides*	Cardinalidae
221	Blue Bunting	*Cyanocompsa parellina*	Cardinalidae
222	Indigo Bunting	*Passerina cyanea*	Cardinalidae
223	Melodious Blackbird	*Dives dives*	Icteridae
224	Great-tailed Grackle	*Quiscalus mexicanus*	Icteridae
225	Black-cowled Oriole	*Icterus prosthemelas*	Icteridae
226	Orchard Oriole	*Icterus spurius*	Icteridae
227	Hooded Oriole	*Icterus cucullatus*	Icteridae
228	Baltimore Oriole	*Icterus galbula*	Icteridae
229	Yellow-billed Cacique	*Amblycercus holosericeus*	Icteridae
230	Chestnut-headed Oropendola	*Psarocolius wagleri*	Icteridae
231	Montezuma Oropendola	*Psarocolius montezuma*	Icteridae
232	Yellow-throated Euphonia	*Euphonia hirundinacea*	Fringillidae
233	Olive-backed Euphonia	*Euphonia gouldi*	Fringillidae
234	Black-headed Siskin	*Spinus notate*	Fringillidae

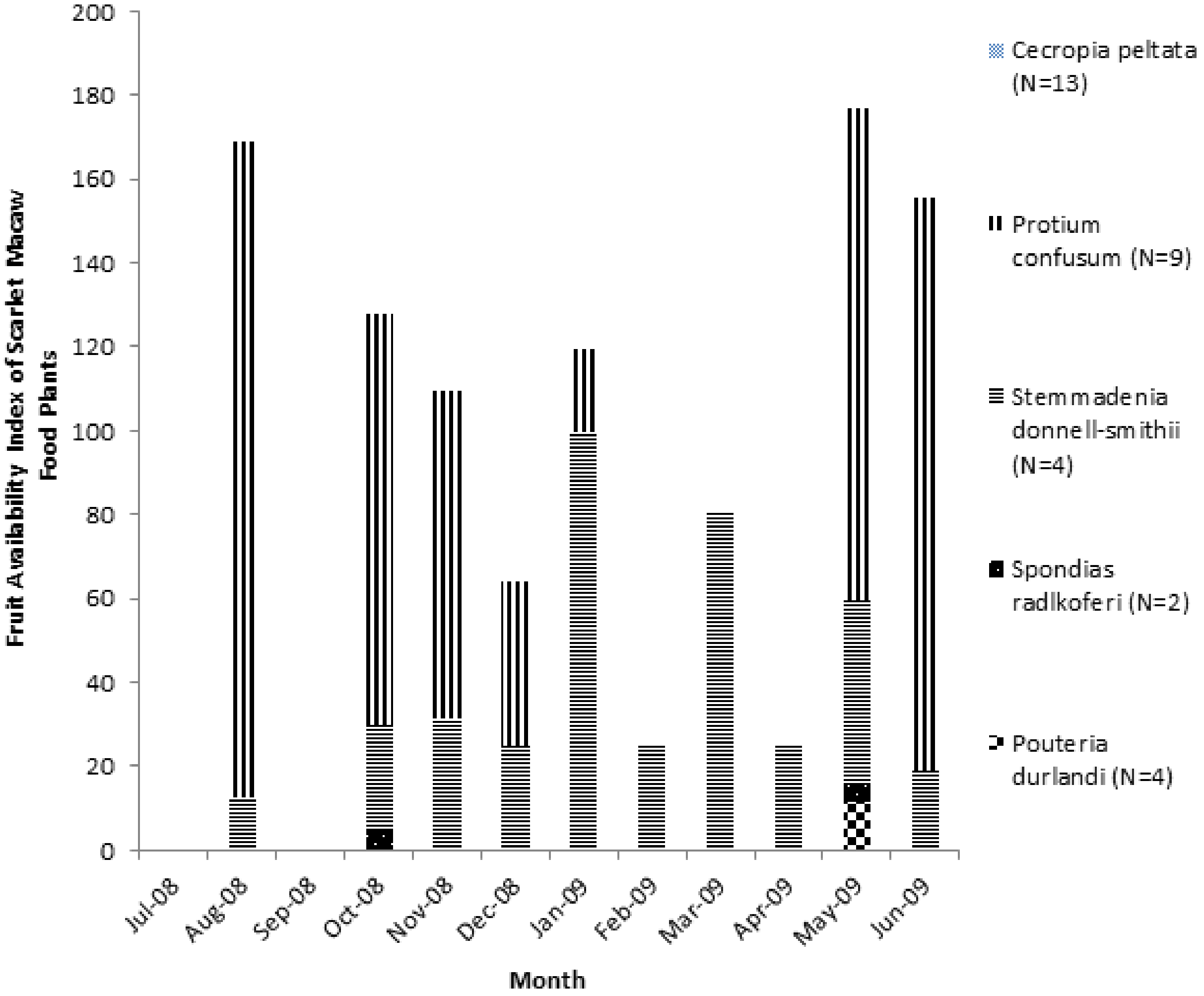
APPENDIX H

PHENOLOGY PLOT FRUIT AVAILABILITY INDEX GRAPHS

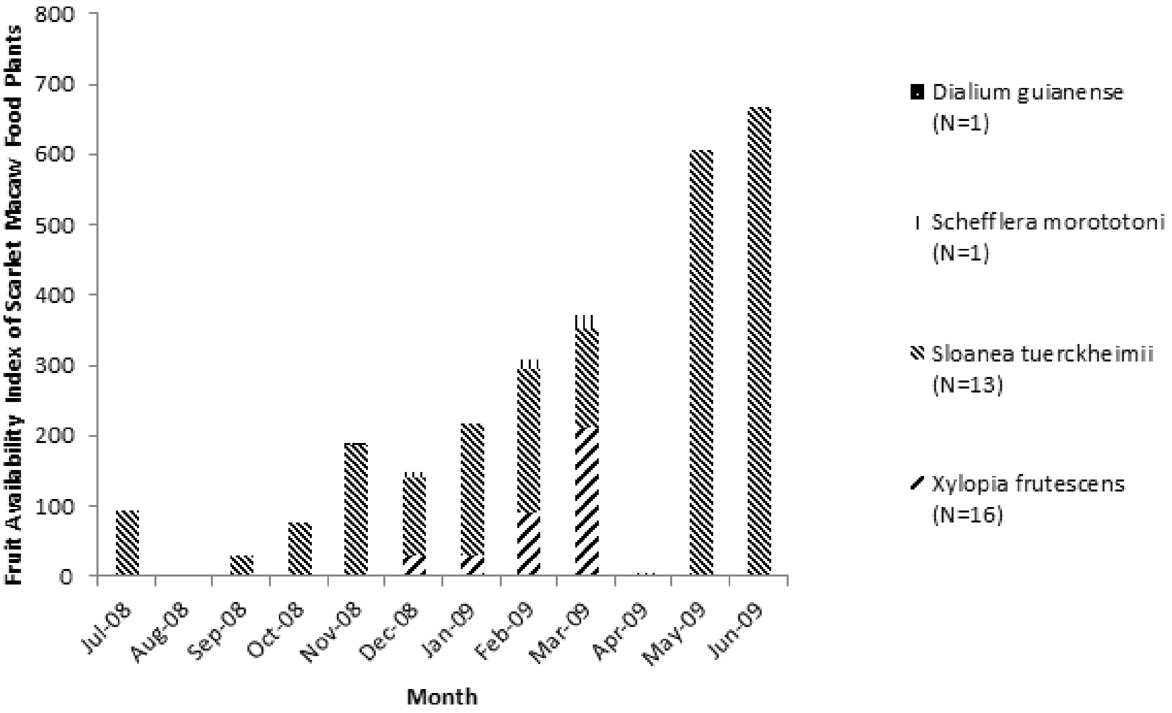
With BFREE as a base, I initially tagged 71 trees in the Maya Mountain Forest Reserve plot. Plot trees known to be Scarlet Macaw food in Belize were *Dialium guianense*, *Trophis racemosa*, *Protium confusum*, *Cordia bicolor*, *Xylopia frutescens*, *Sloanea tuerckheimii*, and *Cecropia peltata.*



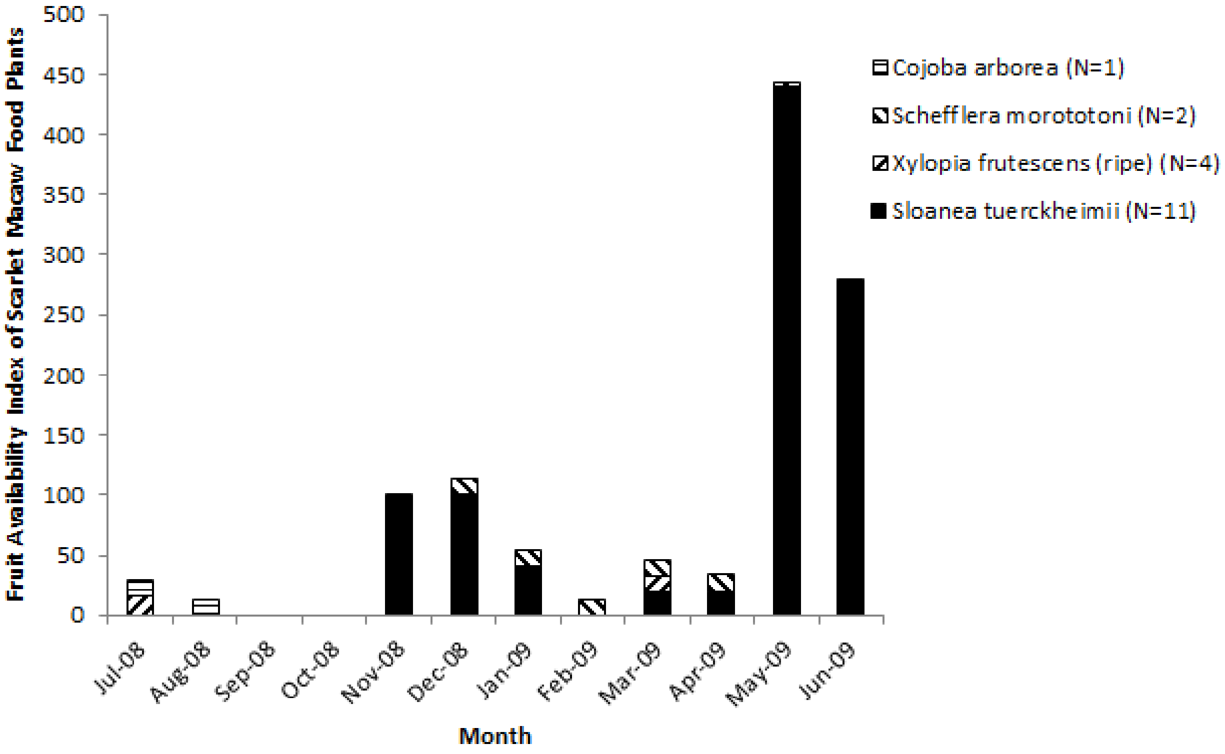
With BFREE as a base, I initially tagged 74 trees in the Bladen plot. Plot trees known to be Scarlet Macaw food in Belize were *Pouteria durlandi, Spondias radlkoferi, Stemmadenia donnell-smithii, Protium confusum* and *Cecropia peltata.*



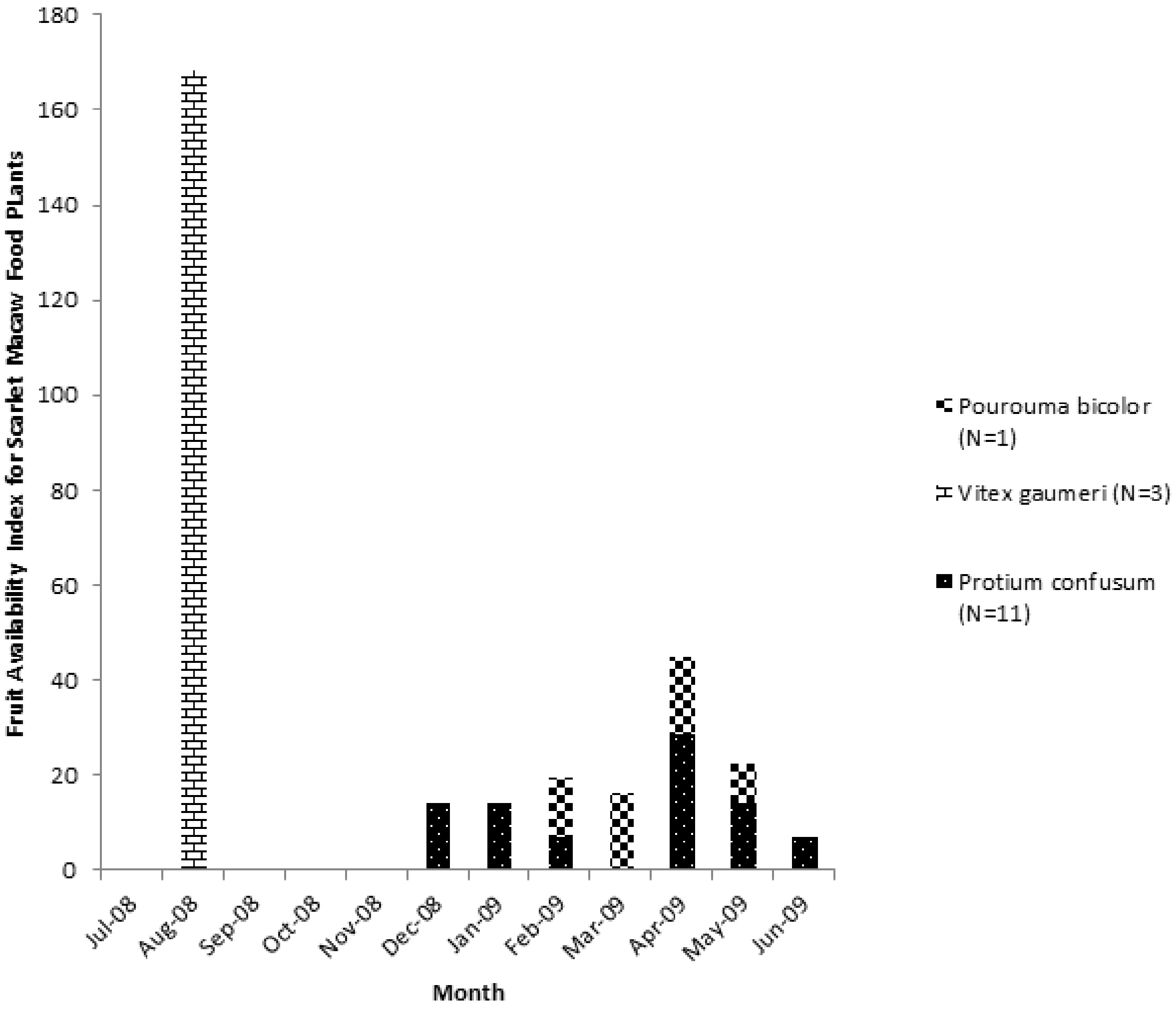
With Red Bank as a base, I initially tagged 44 trees in the Macaw Valley plot. Plot trees known to be Scarlet Macaw food in Belize were *Xylopia frutescens, Sloanea tuerckheimii, Schefflera morototoni* and *Dialium guianense*.



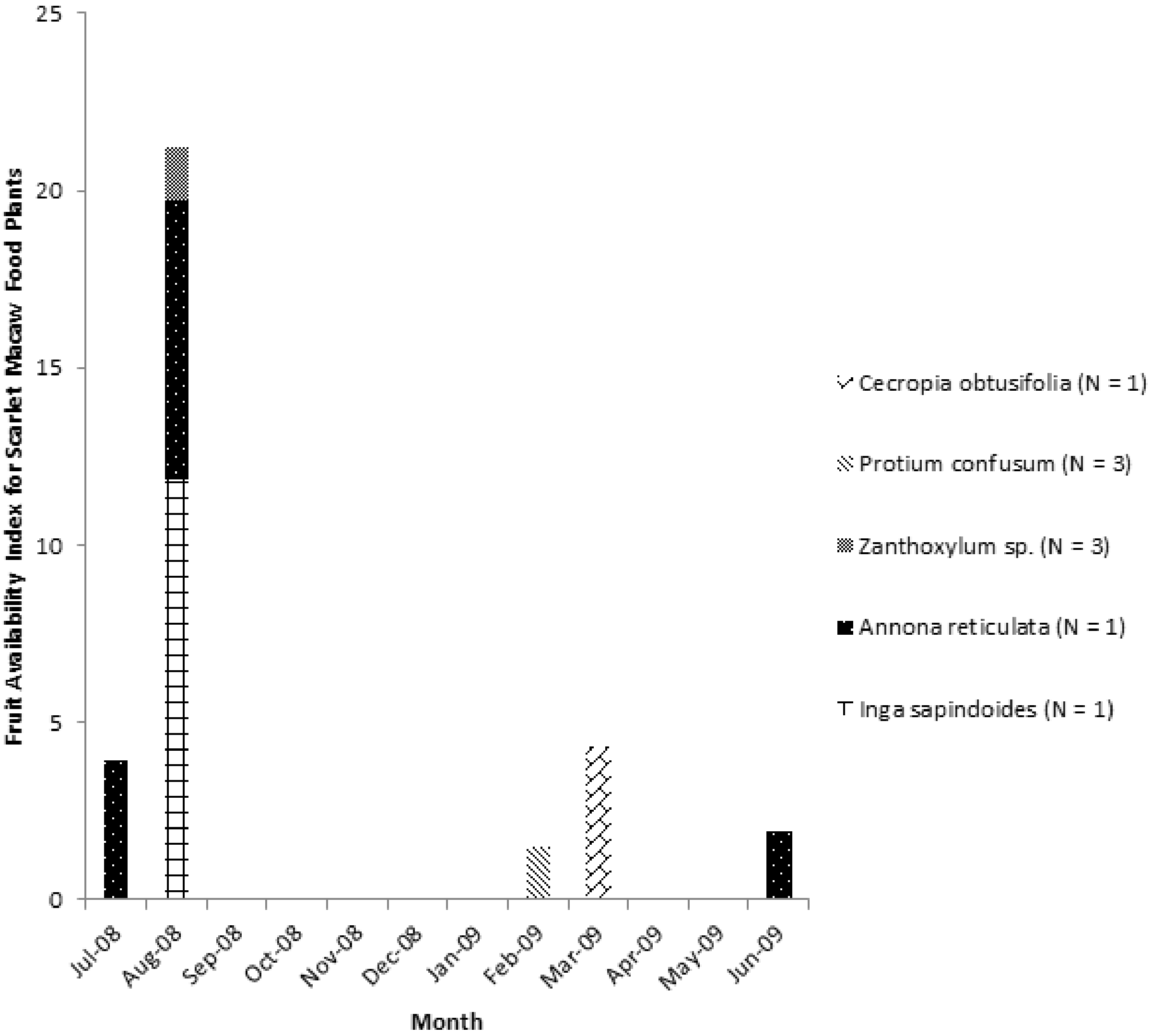
With Red Bank as a base, I initially tagged 26 trees in the Guesthouse Ridge plot. Plot trees known to be Scarlet Macaw food in Belize were *Sloanea tuerckheimii, Xylopia frutescens, Schefflera morototoni,* and *Cojoba arborea*.



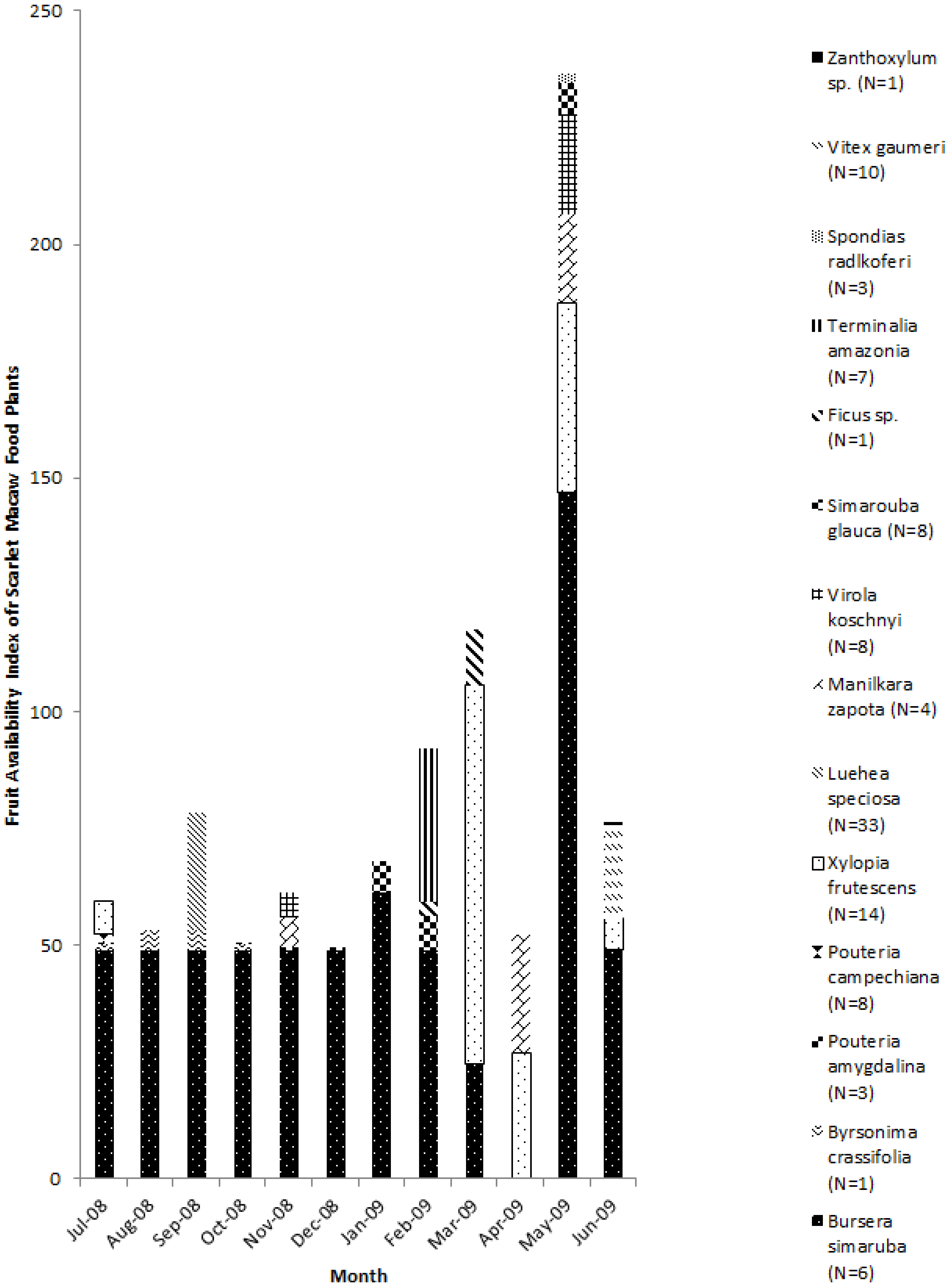
I initially tagged 66 trees in the Mexican Branch Trail plot in the Cockscomb Wildlife Sanctuary. Plot trees known to be Scarlet Macaw food in Belize were *Protium confusum, Vitex gaumeri,* and *Pourouma bicolor.*



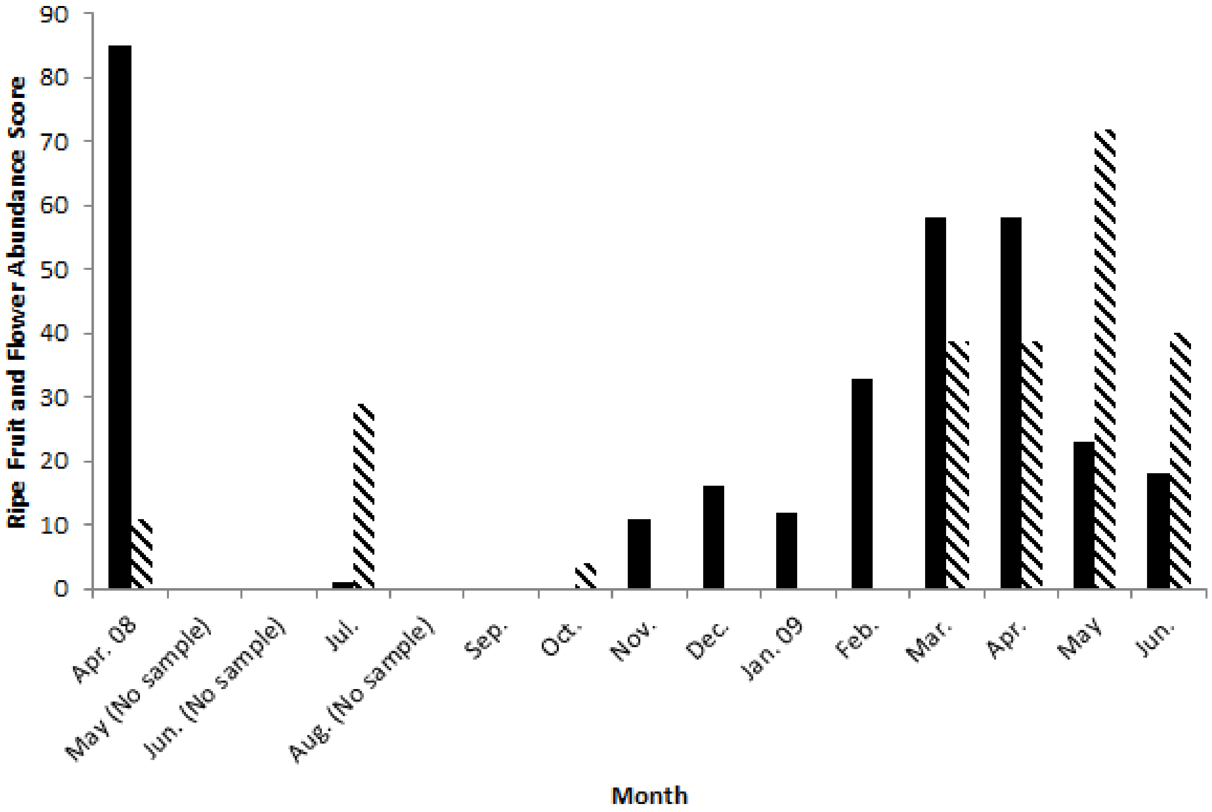
I initially tagged 60 trees in the Snook Eddy Trail plot in the Cockscomb Basin Wildlife Sanctuary. Plot trees known to be Scarlet Macaw food in Belize were *Inga sapindoides, Annona reticulata, Zanthoxylum* sp.*, Protium confusum*, and *Cecropia obtusifolia.*



From the FCD Chiquibul Guardhouse, I initially tagged 191 trees in the Guacamallo Bridge Road plot. Plot trees known to be Scarlet Macaw food in Belize were *Bursera simaruba, Byrsonima crassifolia, Pouteria amygdalina, Pouteria campechiana, Xylopia. frutescens, Luehea speciosa, Manilkara zapota, Virola koschnyi, Simarouba glauca, Ficus* sp.*, Terminalia amazonia, Spondias radlkoferi, Vitex gaumeri* and *Zanthoxylum* sp.


Fruit Availability Index ofr Scarlet Macaw Food Plants
250
200
150
100
50
0
Jul-08
Aug-08
Sep-08
Oct-08
Nov-08
Dec-08
Jan-09
Feb-09
Mar-09
Apr-09
May-09
Jun-09
Month
Zanthoxylum sp. (N=1)
Vitex gaumeri (N=10)
Spondias radlkoferi (N=3)
Terminalia amazonia (N=7)
Ficus sp. (N=1)
Simarouba glauca (N=8)
Virola koschnyi (N=8)
Manilkara zapota (N=4)
Luehea speciosa (N=33)
Xylopia frutescens (N=14)
Pouteria campechiana (N=8)
Pouteria amygdalina (N=3)
Byrsonima crassifolia (N=1)
Bursera simaruba (N=6)

With the FCD Guardhouse as a base, I initially surveyed 71 trees in the Guacamallo Bridge Road Polewood plot. This plot focused only on polewood. An FAI could not be calculated because tree diameter was not measured; however, abundance of fruit and flowers was scored and a graph of flowering and ripeness created: the dark bars are ripe fruit and diagonally striped bars are flowering. March and April ripe fruit results are the same and accurate as the data were rechecked.



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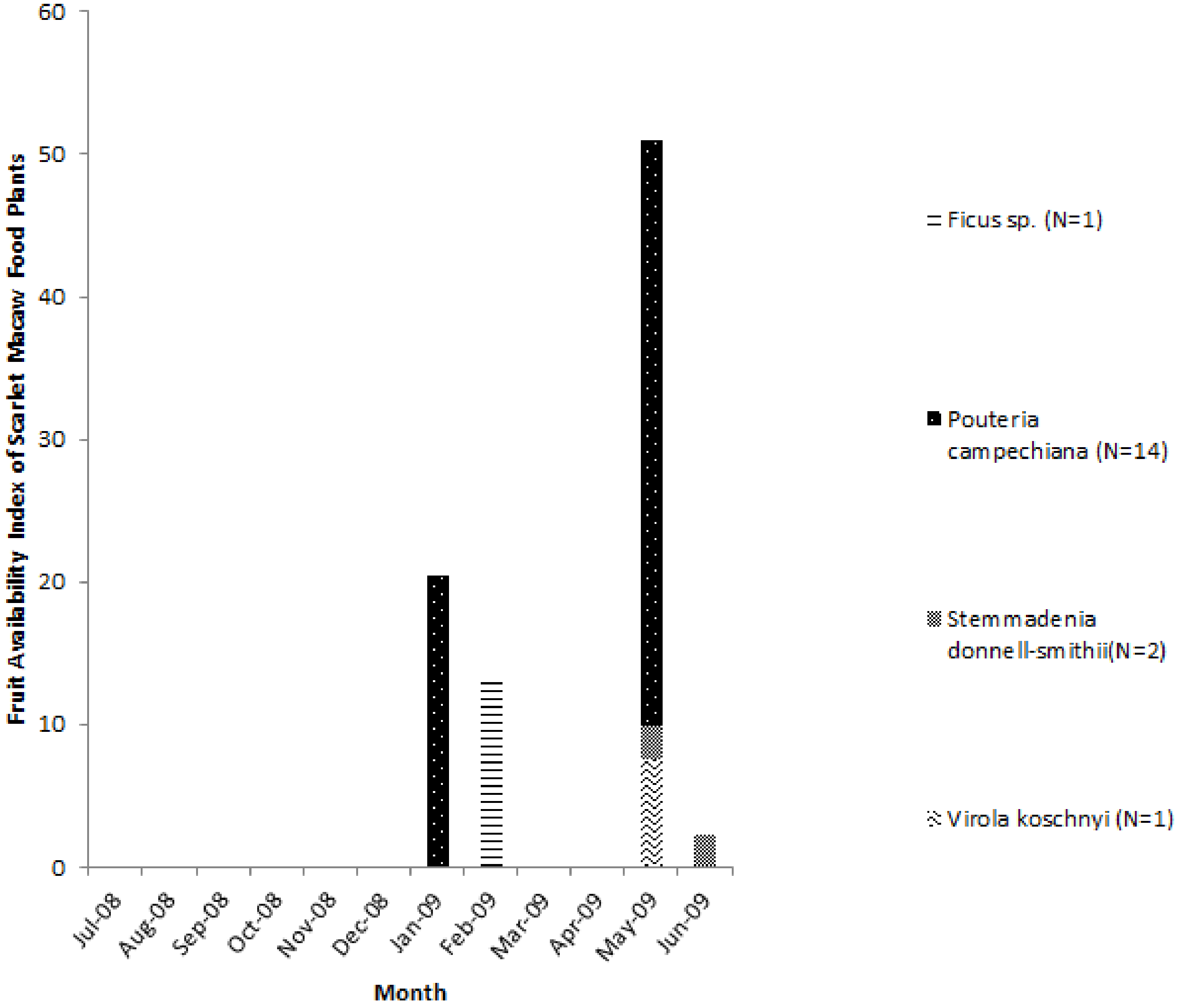
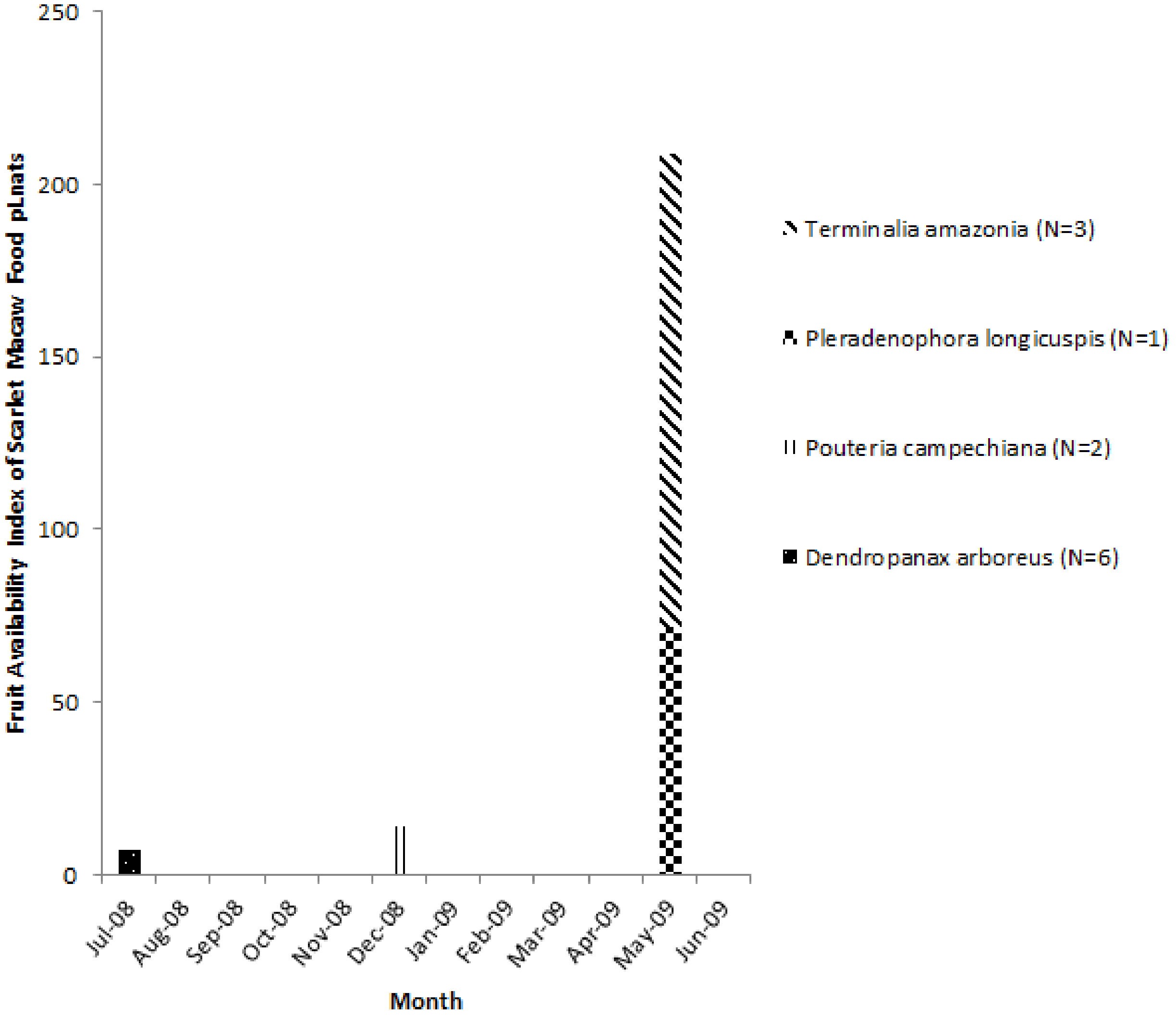
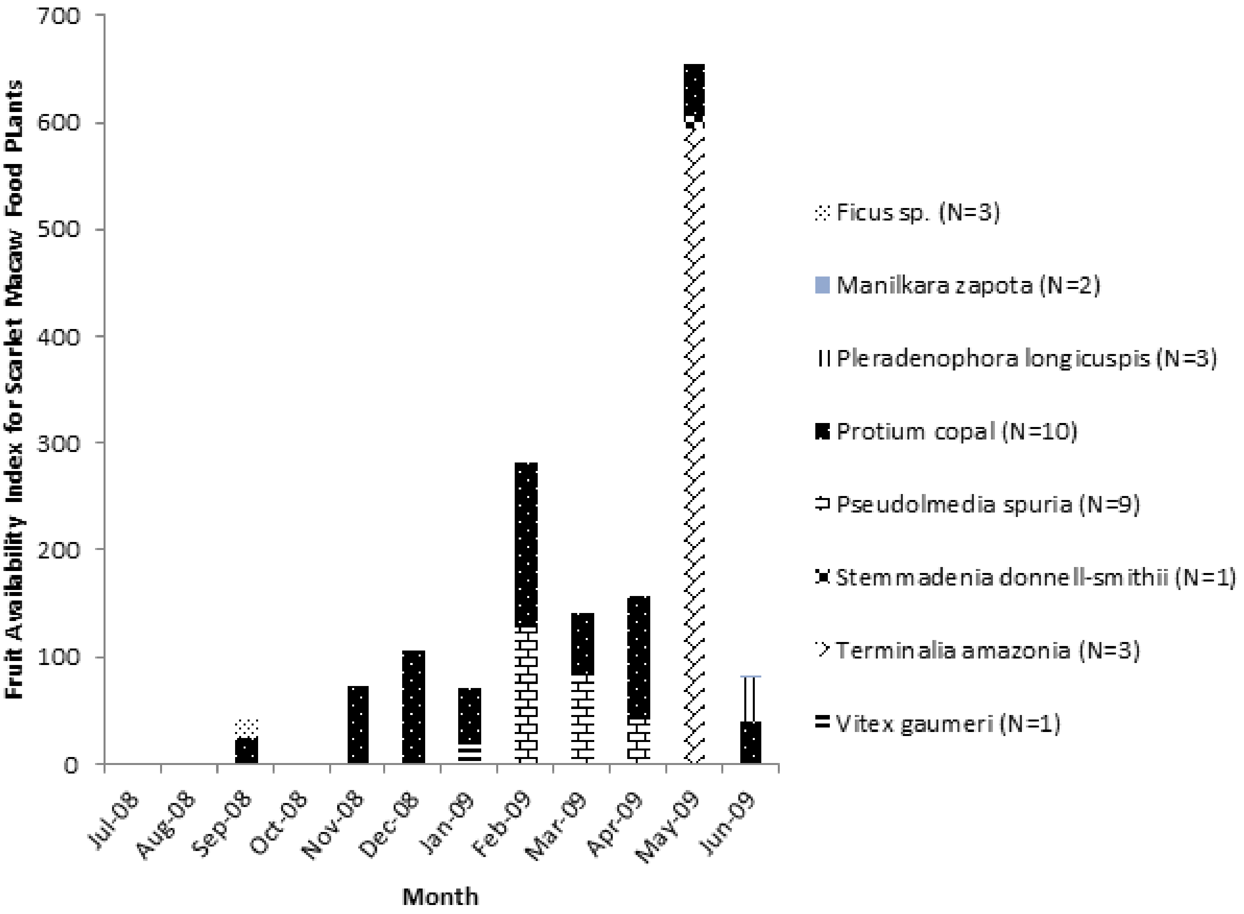
With the FCD Guardhouse as a base, I initially tagged 85 trees in Caracol Road plot. Plot trees known to be Scarlet Macaw food in Belize were *Virola koschnyi, Stemmadenia donnell-smithii, Pouteria campechiana* and *Ficus* sp.



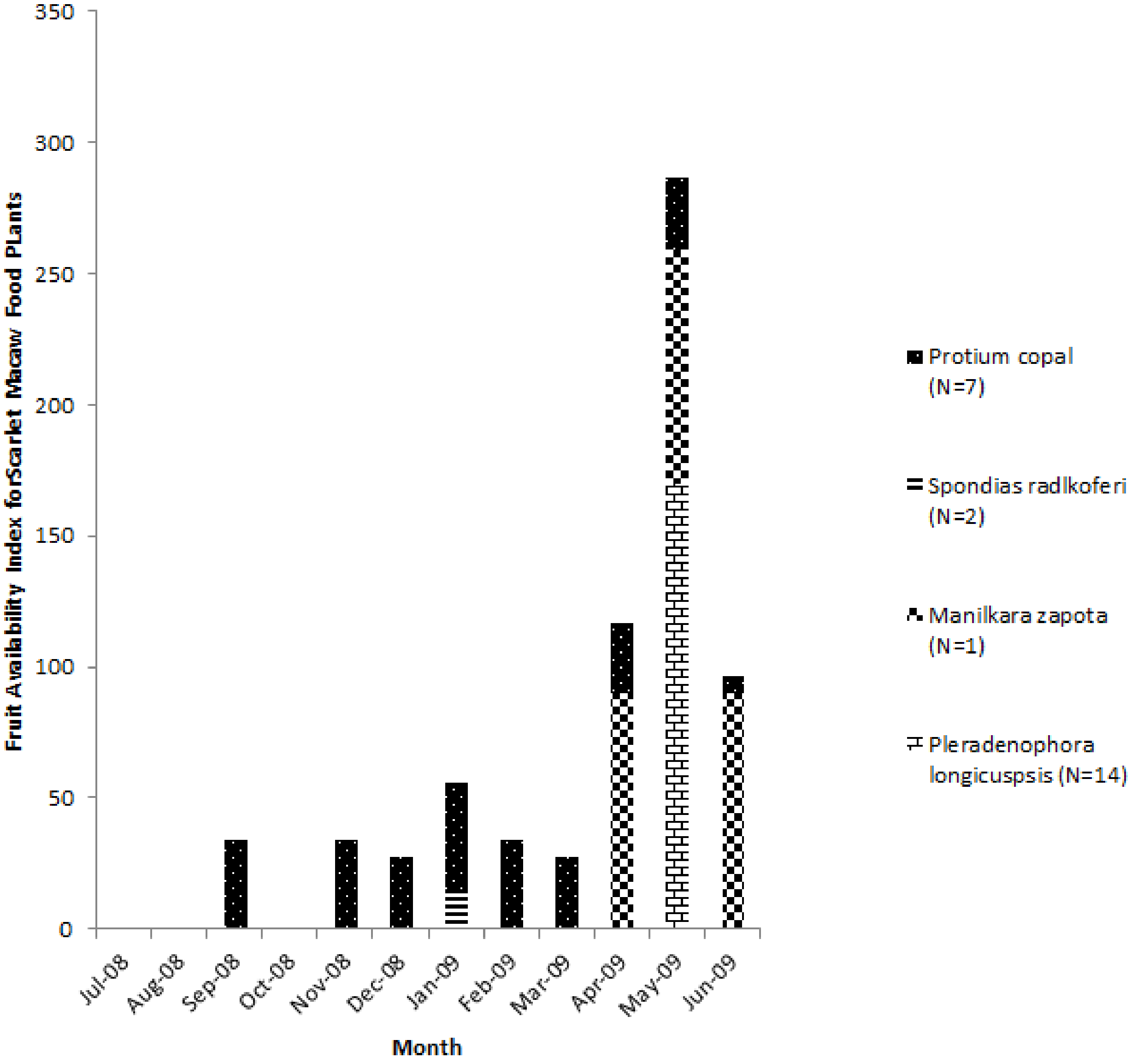
From the Las Cuevas Road, I initially tagged 43 trees in the Cubetas plot. Plot trees known to be Scarlet Macaw food in Belize were *Dendropanax arboreus, Pouteria campechiana, Pleradenophora longicuspis*, and *Terminalia amazonia*.



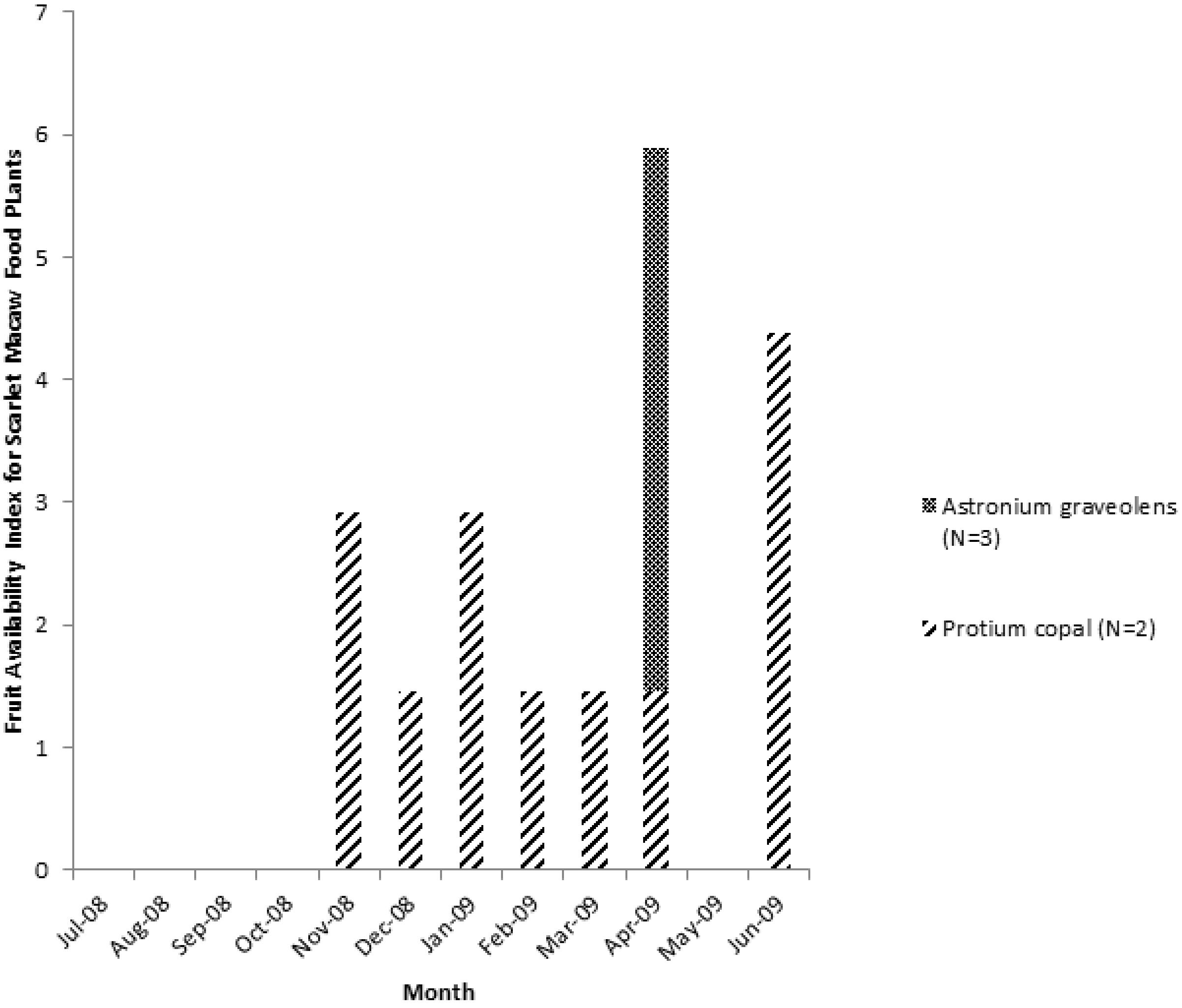
Using Las Cuevas as a base, I initially tagged 61 trees in the Las Cuevas plot. Plot trees known to be Scarlet Macaw food in Belize were *Vitex gaumeri, Terminalia amazonia, Stemmadenia donnell-smithii, Pseudolmedia spuria, Protium copal, Pleradenophora longicuspis, Manilkara zapota* and *Ficus* sp.



Using Las Cuevas as a base, I initially tagged 44 trees in the San Pastor plot. Plot trees known to be Scarlet Macaw food in Belize were *Pleradenophora longicuspis, Manilkara zapota, Spondias radlkoferi* and *Protium copal*.



Using Las Cuevas as a base, I initially tagged 36 trees in the Monkey Tail Trail plot. Plot trees known to be Scarlet Macaw food in Belize were *Astronium graveolens* and *Protium copal*. *Attalea cohune* was also eaten on this plot, but not sampled and so not graphed.



APPENDIX I

PHENOLOGY CHART FOR SCARLET MACAW FOOD PLANTS IN SOUTHERN BELIZE

Species	**Jul.**	**Aug.**	**Sep.**	**Oct.**	**Nov.**	**Dec.**	**Jan.**	**Feb.**	**Mar.**	**Apr.**	**May**	**Jun.**
***Acacia* sp.**											5	1
Annona reticulata	2	2		1			1				1	1
Aspidosperma spruceanum				1						1	1	
Astronium graveolens										1		
Attalea cohune	4						1	1	1	1		4
Bernoullia flammea					2							1
Brosimum alicastrum			1					1	1	2	2	2
Bursera simaruba	2	1	4	2	4	8	8	4	7	8	12	8
Byrsonima crassifolia	1	6	1	1			2		1	1	1	
Calophyllum brasiliense	1			1								1
Castilla elastica				1	1					1		
Cecropia obtusifolia			1				1	1	2	1		
Cedrela odorata					1	1	1	2	1	1	2	1
Ceiba pentandra							1	2	3	6	1	
***Cionosicys* sp.**							2	2	3	2	3	
***Cnidoscolus* sp.**	1	1				1			4		1	

Species	**Jul.**	**Aug.**	**Sep.**	**Oct.**	**Nov.**	**Dec.**	**Jan.**	**Feb.**	**Mar.**	**Apr.**	**May**	**Jun.**
Cojoba arborea	1	2										
Combretum fruticosum								5	4	1		1
Cordia alliodora									1			1
Cordia bicolor				1								
Cymbopetalum mayanum						1		1		1		1
Dendropanax arboreus	3	4		5	2		1					
Dialium guianense	2				1			1	1	3	1	3
Ficus sp.	7	1	2				4	7	8	4	1	2
Guazuma ulmifolia		2	2			3	1	2	3	3	5	
Inga densiflora							3	3	3	3		
Inga edulis		1										
Inga vera	1		1	1					1	1		2
Licania platypus		2			1					1	1	
Licaria peckii	1						1				3	
Luehea seemannii								1	1			
Luehea speciosa		2	2			3	1	1	1		1	1
Manilkara zapota		1			1			1	2	4	3	2
Nectandra sp.		2									1	1
Pera arborea				1	3	4	24	1	9	1		1

Species	**Jul.**	**Aug.**	**Sep.**	**Oct.**	**Nov.**	**Dec.**	**Jan.**	**Feb.**	**Mar.**	**Apr.**	**May**	**Jun.**
Pimenta dioca		1	2		1						1	1
Platymiscium dimorphandrum							2					
Pleradenophora longicuspis			1							3	7	9
Pourouma bicolor								2	2	2	2	1
Pouteria amygdalina	1			1	1	1	1	1		2	1	
Pouteria campechiana	1					1	1	1			1	
Pouteria sapota		1			1				1		3	
Protium copal	2	1	5		7	12	6	8	10	10	10	12
Pseudolmedia spuria								3	2	6	3	
Pterocarpus officinalis					1							
Pterocarpus rohrii				2							1	
Sabal mauritiiformis				1	1							
Schefflera morototoni					1	6	6	3	4	4	3	
Schizolobium parahyba	3						5	4	14	17	10	16
Sideroxylon stevensonii									1			1
Simarouba glauca				1			1	1		1	5	
Sloanea tuerckheimii	9	4	3	6	10	12	25	10	10	4	22	31
Spondias mombin	1		1				2	2	2	2	1	1
Spondias radlkoferi	1	3		3	1	1	3				3	

Species	**Jul.**	**Aug.**	**Sep.**	**Oct.**	**Nov.**	**Dec.**	**Jan.**	**Feb.**	**Mar.**	**Apr.**	**May**	**Jun.**
Stemmadenia donnell-smithii	1	4		2	1	2	3	2	6	1	11	8
Swartzia **sp.**											1	
Swietenia macrophylla		1		1					2	1		
Terminalia amazonia								1		1	6	
Trophis racemosa		1	1	1		2	1	1		2	3	
Vatairea lundellii									3	1		
Virola koschnyi	1				1						3	3
Vitex gaumeri	3	8	3	2			1			1	5	8
Vochysia hondurensis		4										1
Xylopia frutescens	27	14	24	23	39	43	101	55	61	74	36	26
Zanthoxylum belizense							1	1	1	1		
Zanthoxylum ekmanii								3	5			
Zanthoxylum **sp.**		2								1		2

The number in the shaded box indicates how many records of fruit (from all sources) occurred in that month and may not indicate fruit at the ripeness preferred by Scarlet Macaws.

APPENDIX J

SCARLET MACAW FOOD AVAILABILITY AND FEEDING OBSERVATIONS IN THE LOW ELEVATIONS OFSOUTHERN BELIZE.[1]

Dec.	Jan.	Feb.	Mar.	Apr.	May
	Bursera simaruba	*Bursera simaruba*			
Cecropia peltata	*Cecropia peltata*				*Cecropia peltata*
	Combretum fruticosum				
			Ficus sp.		
			Luehea seemannii		
	Pera arborea		*Pera arborea*		
	Platymiscium dimorphandrum				
		Pourouma bicolor	***Pourouma bicolor***	*Pourouma bicolor*	*Pourouma bicolor*
Protium confusum	*Protium confusum*	*Protium confusum*	*Protium confusum*	*Protium confusum*	*Protium confusum*
Schefflera morototoni	***Schefflera morototoni***	*Schefflera morototoni*	*Schefflera morototoni*	*Schefflera morototoni*	
		Schizolobium parahyba	*Schizolobium parahyba*		
Sloanea tuerckheimii	***Sloanea tuerckheimii***	***Sloanea tuerckheimii***	***Sloanea tuerckheimii***	*Sloanea tuerckheimii*	*Sloanea tuerckheimii*
Stemmadenia donnell-smithii	*Stemmadenia donnell-smithii*	*Stemmadenia donnell-smithii*	*Stemmadenia donnell-smithii*	*Stemmadenia donnell-smithii*	*Stemmadenia donnell-smithii*
			Vatairea lundellii		
Xylopia frutescens	***Xylopia frutescens***	***Xylopia frutescens***	***Xylopia frutescens***		*Xylopia frutescens* (minor amount)
		Zanthoxylum ekmanii	*Zanthoxylum ekmanii*		

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[1] Low-elevation sites were Red Bank, Cockscomb, and Bladen Areas. Data from all sources, all years, plus my plot data and point count data. November to April is dry season; May to October is wet season. Non-underlined species are noted if important and having phenology plot records for fruit of any ripeness. Underlined species have feeding records in that month, but not on a phenology plot. Underlined and bolded species have feeding records and phenology plot fruit records.

Jun.	Jul.	Aug.	Sep.	Oct.	Nov.
					Bernoullia flammea
Cecropia peltata		*Cecropia peltata*		*Cecropia peltata*	*Cecropia peltata*
					Licania platypus
Protium confusum		*Protium confusum*	*Protium confusum*	*Protium confusum*	*Protium confusum*
Sloanea tuerckheimii	*Sloanea tuerckheimii*	*Sloanea tuerckheimii*	*Sloanea tuerckheimii*	*Sloanea tuerckheimii*	*Sloanea tuerckheimii*
Stemmadenia donnell-smithii				*Stemmadenia donnell-smithii*	*Stemmadenia donnell-smithii*
		Vitex gaumeri			

SCARLET MACAW FOOD AVAILABILITY AND FEEDING OBSERVATIONS IN THE HIGH- ELEVATION CHIQUIBUL AREA, BELIZE[2].

Dec.	Jan.	Feb.	Mar.	Apr.	May
					Acacia sp.
		Attalea cohune			
Bursera simaruba	*Bursera simaruba*	*Bursera simaruba*	*Bursera simaruba*	*Bursera simaruba*	*Bursera simaruba*
	Byrsonima crassifolia				
	Byttneria catalpifolia				*Byttneria catalpifolia*
			Cecropia obtusifolia		
	Ceiba pentandra	*Ceiba pentandra*		*Ceiba pentandra*	*Ceiba pentandra*
Cnidoscolus sp.			*Cnidoscolus* sp.		*Cnidoscolus* sp.
		Ficus sp.	*Ficus* sp.		
Luehea speciosa					
			Manilkara zapota	*Manilkara zapota*	*Manilkara zapota*
				Pleradenophora longicuspis	*Pleradenophora longicuspis*
				Pourouma bicolor	
	Pouteria amygdalina				
					Pouteria campechiana
					Pouteria sapota
Protium copal	*Protium copal*	*Protium copal*	*Protium copal*	*Protium copal*	*Protium copal*
		Pseudolmedia spuria	*Pseudolmedia spuria*	*Pseudolmedia spuria*	
	Quercus sp.				
	Schizolobium parahyba	*Schizolobium parahyba*	*Schizolobium parahyba*	*Schizolobium parahyba*	*Schizolobium parahyba*
Spondias sp.					*Spondias mombin*
					Swartzia sp.
			Swietenia macrophylla		
					Terminalia amazonia
	Vitex gaumeri				
			Xylopia frutescens	*Xylopia frutescens*	*Xylopia frutescens*

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[2] Data from all sources, all years, plus my plot data and point count data. November to April is dry season; May to October is wet season. Non-underlined species are noted if important and having phenology plot records for fruit of any ripeness. Underlined species have feeding records in that month, but not on a phenology plot.

Jun.	Jul.	Aug.	Sep.	Oct.	Nov.
		Annona reticulate			
Attalea cohune	*Attalea cohune*				
			Brosimum alicastrum		
Bursera simaruba	*Bursera simaruba*	*Bursera simaruba*	*Bursera simaruba*	*Bursera simaruba*	*Bursera simaruba*
	Byrsonima crassifolia	*Byrsonima crassifolia*	*Byrsonima crassifolia*	*Byrsonima crassifolia*	
Calophyllum brasiliense					
		Cnidoscolus sp.			
Cordia alliodora					
	Dendropanax arboreus			*Dendropanax arboreus*	*Dendropanax arboreus*
	Dialium guianense				
Ficus sp.	*Ficus* sp.		*Ficus* sp.		
		Guazuma ulmifolia			
				Inga vera subsp. *spuria*	
	Licaria peckii	.			
			Luehea speciosa		
Manilkara zapota					*Manilkara zapota*
		Nectandra sp.			
Pleradenophora longicuspis					
Protium copal			*Protium copal*		*Protium copal*
				Pterocarpus rohrii	
Schizolobium parahyba	*Schizolobium parahyba*				
Spondias mombin	*Spondias mombin*				*Spondias* sp.
				Trophis racemosa	
	Virola koschnyi				
Vitex gaumeri	*Vitex gaumeri*	*Vitex gaumeri*		*Vitex gaumeri*	
Xylopia frutescens					

APPENDIX K

MAJOR FOOD PLANTS IN BELIZE

Polewood. Based on my records and the records of others (≈ 79 unique sites), polewood ranges from 7.3 m to 1040 m in elevation and occurs widely throughout the study area. Polewood is common in the Mountain Pine Ridge area (Means 1997; Penn et al. 2004), especially in open savanna with pine and grasses and at edges of gallery forests, something easily seen on my many trips through the area to the Chiquibul. Despite an abundance of polewood in the Mountain Pine Ridge, macaws are almost never seen there now, though four were seen in Mountain Pine Ridge feeding on polewood Apr. 12, 2009 along the Francelia Line, approximately 1.5 km from the Macal River, and two were seen feeding on polewood May 16, 2009 along the Kinloch Line, approximately 2 km from the Macal River (Martinez, pers. comm. 2010). Polewood is in the Chiquibul forest (Bridgewater et al. 2006a), a major habitat region for the macaws, though I never saw polewood there except along the Macal River where it was relatively common near Guacamallo Bridge. Polewood is commonly encountered in the high ridges of the Maya Mountains in the “Broadleaf: Class 4, Semi-evergreen forest (highland),” and this type of forest covers the “main watershed of the Raspaculo Branch and Monkey Tail Branch and a large percentage of the watershed of the upper Macal River” (Penn et al. 2004) – all prime macaw habitat. Polewood has also been reported by others in the upper Macal (Matola 2001) and as common in the upper Raspaculo (Brokaw 1991). Polewood is also in the San Pastor pine savanna just south of Las Cuevas with an absolute density of 14 stems per ha in the Fringing Oak woodland (Hicks et al. 2011). Polewood is also present in the understory of the coastal savanna (Bridgewater et al. 2006a; pers. obs. 2009) and at higher-elevations along the Hummingbird Highway (pers. obs. 2009). Polewood is a canopy tree in the poor soil in the Macaw Valley/Red Bank area (pers. obs. 2009). Abundant polewood was eaten by macaws in Cockscomb on Feb. 4, 1986 (Kamstra 1987) and high numbers of polewood line the Victoria Peak Trail, probably because the trail is an old logging road and thus in a disturbed area (pers. obs. 2009).

W. A. Schipp mentioned in 1929 that polewood received its common name from its use in poling dories on rivers (Tropicos.org 2010). Now it is in demand for the ceiling rafter poles, often no more than 15 cm in diameter, used in traditional palm thatch-roofed Mayan and Ketchi (or Kekchi) houses (pers.

obs. 2009). Both immature fruits and flowers are susceptible to removal by strong winds (Sho, pers. comm. 2008; pers. obs. 2009) and a honey bee was seen pollinating flowers June 19, 2009 on the Guacamallo Bridge Road Polewood plot (pers. obs. 2009). The largest polewood I encountered was near the Snook Eddy Trail plot and measured 77 cm dbh.

Wild Annatto. Wild annatto, (*Sloanea tuerckheimii*), also spelled "anatto" and "atto," possibly from "an atto," is a major Scarlet Macaw food at Red Bank, Belize. It has been noted as a food for adult and nestling macaws in Belize during the breeding season (February to June) (Renton 2006) and for adults in Red Bank (Renton, pers. comm. 2011). Within Belize, *Sloanea tuerckheimii* is restricted to southern districts (Tropicos.org 2010). Based on my observations and other records (≈ 75 unique sites), wild annatto occurs throughout the study area and from 9.3 m to 1,040 m in elevation. It is one of the "dominant" trees in the Bladen Nature Reserve on limestone along the river according to a record by D. E. Atha (Tropicos.org 2010). Although it occurs in the Chiquibul (Bridgewater et al. 2006a), I have no records of macaws eating wild annatto there except one listing by A. Howe (King 1998a). It is not a food tree in the Chiquibul, possibly because it is not a canopy species there and macaws prefer to eat in the canopy (Bol, pers. comm. 2009). At Red Bank, in the poor soil, trees do not grow tall and wild annatto is a canopy tree. In a study of forest understory in Belize, seedlings of *Sloanea tuerckheimii* were more abundant in areas with less light in a riparian area (MacDougall & Kellman 1992); polewood and quamwood prefer well-lit forest openings.

The spiky fruits of wild annatto resemble the annatto (*Bixa orellana*) (International Institute of Tropical Forestry 2011), eaten throughout Central America as a paste called *achiote* (pers. obs. 2009). I have no knowledge of the human edibility of wild annatto.

Quamwood. The correct scientific name for quamwood is *Schizolobium parahyba* (not *Schizolobium parahybum*) (Kamau et al. 2003; Marcati et al. 2008; Tropicos.org 2010). It is a major food for nestlings and adults in Belize (Renton 1998b, 2006). Quamwood has an "irregular, clumped distribution" (Bird 1998), and can be found in watershed basins in large groups as at Sapote Creek near Red Bank, or at Zayante and Cotton Tree creeks near Guacamallo Bridge in the Chiquibul. *Schizolobium parahyba* occurs not only in riparian zones, however, as it is also "common on the ridges" as seen from the "Victoria Peak Trail: Trail Base camp at 12 km to Waterfall Camp at 19 km". (Meerman 2010).

After reading about the controversy over the Chalillo Dam flooding of quamwood nest trees, I expected quamwood to be rare. Rather, it is as common a constituent of the forests in southern Belize as it was in 1932 when W. A. Schipp noted that it is "one of the tallest of forest trees and a most wonderful sight when in flower" (Tropicos.org 2010). From my records and the records of others, quamwood is common within the study area (≈ 78 unique sites) and occurs from 7.5 to 800 m. Looking for flowering quamwood while flying over the Chiquibul area in mid-February, Britt reported that much of this species occurred in the forest (Britt 2010a). In the Chiquibul, it is among the dominant trees in the Broadleaf: Class 4, Semi-evergreen forest (highland), which includes the watershed of the upper Macal, Raspaculo and Monkey Tail. It is also a dominant tree in Broadleaf: Class 2a, Seasonal high forest; Broadleaf: Class 15, Alluvial forest; and Riparian: Class 16 Riverine forest (Penn et al. 2004). I have records of quamwood occurring from 7.3 m to 660 m in elevation. It is a fast growing species (Standley & Steyermark 1946; Rachie et al. 1979) and unlike some tropical trees has annual rings, with the darker areas representing the dry season and leaf loss (Marcati et al. 2008). The heartwood's susceptibility to decay and insects (Record & Hess 1943) probably assists in making cavities for macaw nests; quamwood is a preferred nest tree.

Quamwood is shade-intolerant (Bird 1998), a pioneer (Rachie et al. 1979), and "a conspicuous colonizer of gaps in the forest" in the Chiquibul (Johnson & Chaffey 1973). Quamwood loses its leaves and flowers in the dry season; its blooms are a bright yellow and quite conspicuous. Flowering occurs usually in January and February, but has also been observed in mid-March (Meerman 2010). Quamwood is a legume and not a valuable lumber tree, but it has been logged in the Chiquibul area (Bird 1998). This tree is sometimes called quam or quan after the Guan or Curassow, which is said to eat its seeds (Standley & Steyermark 1946). I was able to watch a Crested Guan eat quamwood flowers on Feb. 28, 2009 along the Snook Eddy plot in Cockscomb.

<u>Wild Chaya</u>. Seeds of the genus *Cnidoscolus*, common name wild or stinging chaya, have been noted as an important food for adults and nestlings (Renton 2006). There are six species in the genus within Belize, *C. acontifolius*, *C. chayamansa*, *C. tubulosus, C. multilobus*, and *C. souzae* (Tropicos.org 2010); and an additional record of *C. schiedeanus* along the Macal River edge (Urban et al. 2006). There is only one record of *C. acontifolius* within the Chiquibul, along the Macal River (Urban et al. 2006), and

C. chayamansa has no records there; both have records in surrounding areas, generally in disturbed or second growth areas. *C. tubulosus* is described from two sites, one in the Chiquibul, as being in a disturbed area and by a river. Both *C. multilobus*, and *C. souzae* are in the Chiquibul (Bridgewater et al. 2006a). Two of nine records associate *C. multilobus* with riparian habitats and the three records for *C. souzae* all indicate a preference for disturbed areas.

Mo tree. The mo tree, first identified as *Pera barbellata* (Meerman 1999) and then as *Lacistema aggregatum* (McRae 2000) was determined to be *Pera arborea* by my work, which has been confirmed (Brewer, pers. comm. 2009). With approval from J. Sho, I created a new common name for it: mo tree. The word “mo” means macaw in Maya and I believe “mo tree” is a satisfactory replacement for “macaw feeding tree,” the literal translation into English from the Ketchi (Kekchi) Maya language. My records, and the records of others (≈ 63 unique sites), indicate that this tree is found from 6 m to 184 m. With no mention of this species in the literature for the Chiquibul area (Penn et al. 2004; Bridgewater et al. 2006a; Brokaw et al. 2007), this may be a lower-elevation tree. Although not found in my Red Bank plots, the mo tree is common and is an important food tree that may fruit biennially.

Cohune Palms. The importance of cohune palms (*Attalea cohune*) became apparent during the course of my study. They were not on the initial list of food plants I used to determine which trees to sample on plots, but I did observe macaws eating cohune palm nuts once and now have records of several similar observations (Bol & King 1996; King 1998a; Matola & Sho 1998; Renton 1998a, 1998b; Minty 2001). In my records and the records of others, *Attalea cohune*, a very common tree, has been found from 10 m to 627 m in elevation. I have records of macaws scraping off and eating the epicarp of the “nut” in the months of February, June, and July, as well as in March and April (Gentle, pers. comm. 2009). To the north in Rio Bravo, Belize, cohune palms flowered from January to July and some had “nuts” year-round (Hess 1994). Timing may differ in the study area. Chiquibul fruit availability peaked in May and June in this study and those months are the ones with the most sightings of cohune palm nut feeding, but the abundance of cohune palms and year-round fruit means they may be a year-round food resource for macaws. One problem is that, although rodents can chisel through the cohune palm nut and into the nut meat, macaws do not, and so derive such small caloric content from these nuts that other foods would seem to be more efficient to feed on. In Guatemala, feeding on cohune palm nuts is said to be done to prevent excessive beak growth, much like gnawing of the internal skeleton of cuttlefish does for parrots in cages. One study found “exceptionally high” concentrations of sodium in *Attalea cohune* leaves (Arnason et al. 1984); perhaps the nuts are also high in sodium and macaws eat the outside of the nuts because they need or want the sodium.

APPENDIX L

CONSERVATION CONCERNS AND SOLUTIONS

HABITAT ISSUES

In the Chiquibul area of Belize the existing macaws can find adequate food but perhaps not enough trees adequate for nesting. Unsustainable logging in the Chiquibul area (Bird 1998) has deprived macaws of many actual and potential nest cavities. Quamwood, the preferred tree for nesting, should not be logged at all. Quamwood is not a highly sought-after hardwood like mahogany (*Swietenia macrophylla*) and cedar, so with selective removal of these species (the preferred silvicultural practice) it should not be economically difficult to leave quamwood trees of all age classes standing. Leaving a percentage of all large trees in logged areas would make them available for snag production (Gibbs et al. 1993), and possible macaw nests. King (1998a) proposed surveying for macaw nests in logging areas before activity occurs and when the macaws are nesting (King 1998a). Both logging and macaw nesting occur in the dry season, so nest surveys should be done the previous season, with at least a cursory survey in December and while logging.

Other anthropogenic habitat loss could be minimized. In December and January, the beginning of the macaw breeding season, small arms fire, even with blanks, near Guacamallo Bridge by British Forces and the BDF, probably renders much of the extensive quamwood habitat in Cotton Creek unavailable to macaws as a nesting and feeding area. More riparian areas could be made available for nesting. Habitat damage done by dam building may have run its course in the Chiquibul, but hydroelectric dams could go up elsewhere. A dam proposal in the Bladen Reserve is currently being fought by the Ya'axché Conservation Trust and others. That project is located in a reserve not even open to the general public because of its scientific value (Wicks et al. 2010).

At Red Bank, habitat could be enhanced by creating a nursery for polewood, mo tree, and wild annatto to provide trees for reforestation. Planted polewood trees in Red Bank might create more food, easier viewing, and eventually poles for roofs and firewood. Stopping fires caused by arson or negligence in the hills of Red Bank is hampered by unrestricted logging and firewood gathering of polewood and wild annatto. At present only a few villagers there have an appreciation for the macaws; social pressure, assisted by environmental education, might eventually turn things around. Banning use of wood as a fuel is highly unlikely unless the hills become part of a protected area.

POACHING AND CAPTIVE BREEDING

The most pressing danger for the Scarlet Macaw population in Belize is poaching. Possible short term “solutions” include preventing or reducing access to the area, preventing tree-climbing, guarding trees likely to be poached, getting birds before poachers do and releasing them later, and effective prosecution of poachers. The Chiquibul stronghold of macaw breeding is very large and remote and its border with Guatemala is quite porous. The present road network is often overgrown and impassable by enforcement vehicles. Although conservationists often oppose roads, maintaining existing dirt roads would probably reduce poaching by enabling enforcement patrols to gain access to many areas of the Chiquibul. Poachers move by foot or horse along their own trails. They would expose themselves when using the maintained roads. Of course the logging industry might also support road maintenance to further unsustainable harvesting of timber.

The agencies that patrol the Chiquibul, the Friends for Conservation and Development (FCD) and the Belizean Defense Forces (BDF), are outnumbered. Motivated and trained FCD rangers do patrol, but they are few in number and lack reliable vehicles. More vehicles, more rangers, and more than one ranger post would be a huge improvement for the entire area. The effectiveness and frequency of the BDF patrols are reduced by the men’s dislike of the remoteness of this posting and by their lack of knowledge of the area. Las Cuevas and Rio Blanco have BDF outposts. More outposts would help, along with the recruitment of some individuals who would become experts in the area and lead new patrols in the same way that BDF soldiers assist British and U.S. forces in their jungle training.

If, as in Guatemala, the situation can be considered a conservation “war,” the military should have a role in it. *Xateros* from Guatemala are considered armed and hostile towards Belizean authorities (Meerman & Moore 2009). U.S. and British forces conducting jungle training generally stay in predictable locations, which are easily avoided by the *xateros.* Having the U.S. and British forces move about the area in unpredictable ways would make the area less hospitable to *xateros.* So would embedding Belizean authorities with the power to arrest *xateros*. If the U.S. and British forces were to take a more active part in this “war,” they could carry out conservation patrols, apprehend *xateros* (usually easily distinguished from Belizeans by language), and leave them to the care of the Belizean troops attached to them. More passively, U.S. and British forces could conduct nighttime overflights to locate cooking fires or concentrations of people and pack animals via thermal imaging, relaying coordinates to Belizean or joint patrols.

Patrols with dogs would also be a clear deterrent. Dogs could be trained to warn of intruders at nest-guarding sites, track *xateros*, or track horses transporting *xate* back to Guatemala. News of "attack dogs" might be announced by signs to worry *xateros*. Dogs controlled by ultrasonic whistle could even be sent into suspected *xatero* camps, avoiding potentially hazardous situations for rangers. Dogs have been used successfully for research purposes within Belize even in areas of high jaguar concentration (Wultsch, pers. comm. 2009).

In addition to better detection of poachers, more effective prosecution of poachers is necessary. Stories of captured *xateros* being released to go back to Guatemala, and with their *xate*, have circulated. The legal system looks at the *xateros* as merely illegal immigrants, of which there are many in Belize. If *xateros* were jailed for breaking wildlife laws until a fine was paid, poaching would be much less lucrative. Another possibility discussed by WCS Guatemala is to microchip chicks so that if they are poached they can be identified (Boyd 2008).

An additional layer of defense is to prevent the physical act of poaching. One method would be to discourage the physical climbing of nest trees. Placing regular barbwire around nest tree trunks has been tried in Guatemala, but was found to harm the tree (Villeda 2000); concertina barbwire might work better expanding with tree growth. It might be worth trying to place noxious substances on the trunks, such as natural oils (poison wood oil), irritating dusts, dyes, or natural rubber. Fluorescent powders on the trunk or the ground might make tracking of poachers easier. Solar electric powered shock wires or a tripwire that triggers the dumping of a noxious substance (human excrement?) on tree climbers might also be deterrents.

Another possibility to prevent poaching of accessible trees is to close nests highly likely to be poached as is done in Venezuela with parrots (Briceno-Linares et al. 2011) and in Costa Rica with Scarlet Macaws (Vaughan et al. 2003b). These nests would likely be near areas of high *xatero* traffic (they have regular trails) and would possibly include the drowned trees in the Chalillo Dam reservoir, and nest trees along the shore easily accessed via raft or boat. Closing the nest cavity entrance via plastic wrap or wood boards would force the macaws to nest elsewhere, and would be far better than certain poaching, both for that nesting pair and for the species.

Guarding nest trees is another possibility and has been done with relative success in Costa Rica and Guatemala (Vaughan et al. 2003b; Boyd & McNab 2008), and in Venezuela with parrots (Briceno-Linares et al. 2011). Providing 24 hour surveillance protection is expensive. Self-funded (probably foreign) volunteers are also a possibility, but in such remote sites they too might need protection from armed *xateros*. Macaw eggs are of little interest to poachers, so any nest-guarding and intensive patrols should start in March, when most chicks have hatched, and should continue through June, when most nestlings have fledged. This strategy will leave the early and late chicks vulnerable, but may protect the majority of chicks. Nest-guarding should be done at trees with cavities that have been in use in previous years.

Removal of excess chicks, or chicks in unsafe nests, should also be considered. Based on eleven years of research, reports from Peru concerning *Ara m. m.* state that 96% of the third chicks and 100% of the fourth chicks in the nest die from malnutrition (Brightsmith & Vigo-Trauco 2010). In Belize (Britt 2010e) and Guatemala (Villeda 2000; Garcia et al. 2004; Britt 2010e), only one or two macaw chicks fledge. Chick removal worked with parrots when the nestlings were removed every night and then returned in the morning (Briceno-Linares et al. 2011). Removal of all chicks and placing them in a captive breeding situation would also eliminate poaching. Chicks could be raised and released as is being done in Costa Rica (Janik et al. 1999; Brightsmith et al. 2003; Matuzak 2004b; Forbes 2005) and is seriously being considered in Guatemala (Boyd & McNab 2008) and El Salvador (Bjork 2008; Bjork & Komar 2008; Boyd & McNab 2008). Removing the third or fourth chick for future reintroduction or captive breeding would also increase food for the remaining nestlings.

In Belize, keeping chicks for breeding purposes would be expensive, requiring trained staff, adequate facilities, and long-term institutional commitment. The Belize Zoo is one possibility because it is most likely to be able to find and maintain the expertise needed to keep Scarlet Macaws; the zoo has already been caring for Scarlet Macaws for a number of years. Another possibility is the Ara Macao Resort at the northern end of the Placencia Peninsula, if it is actually built. Ara Macao Resort has committed to a facility for Scarlet Macaws and the CEO professes a love of Scarlet Macaws (Belize

Department of the Environment 2007; Ara Macao Resort and Marina 2010). Belize Bird Rescue is also possible location, though it may have more funding difficulties than either of the two other options (Belize Bird Rescue 2010). DNA identification and genetic analysis can assist with prevention of endogamic problems in captive breeding and reintroduction programs ensuring that birds genetically adapted to the area are used in reintroductions (Feria & de los Monteros 2007a).

Ideally chicks would be released after a year. Soft releases have been occurring in Costa Rica (Brightsmith et al. 2003; Jimenez 2008; Thewissen 2011) and are planned in Guatemala (Boyd & McNab 2008). In the Chiquibul, releases could occur in May or June when large numbers of macaws are present. X*ateros* have stolen or destroyed research equipment in the Chiquibul (including mine), so the release site will need to be very well guarded to prevent theft of these reintroduced macaws. Information on current or planned Scarlet Macaw reintroduction programs can be obtained from the following articles: (Higgins et al. 1999; Janik et al. 1999; Brightsmith 2000; Hilburn & Higgins 2001; Brightsmith et al. 2003; Janik et al. 2003; Martinez 2004; Matuzak 2004a, b; Cornejo et al. 2005; Forbes 2005; Bjork 2008; Boyd & McNab 2008; Jimenez 2008; Macaw Conservation 2009; The Ara Project 2010; Thewissen 2011).

I believe that funding for breeding and reintroduction is more likely than for monitoring or nest-guarding efforts because the aviculture community in the U.S. can much more easily be attracted to a breeding and reintroduction project. Long-term solutions to poaching will require environmental education in both Belize and Guatemala, a general strengthening of enforcement activities related to natural resource conservation and, outside the scope of this paper, development that raises the standard of living for Guatemalans so that they do not need to come to Belize for work.

ARTIFICIAL NEST BOXES AND NEST MONITORING

All indications are that the artificial nests along the Macal and Raspaculo placed as mitigation for the Chalillo Dam are not in use and are not being maintained. Arboreal termites have taken over some nests (Gentle, pers. comm. 2009). Wasps and bees are another problem, although parrot researchers have smoked bees out of cavities with success and attached plastic to the baffle of artificial nests to lessen attachment by bees (Richards 2010). Wasps have been prevented from attaching to nest roofs by placing plastic on the upper inside surfaces of the artificial nests (Hoser, pers. comm. via NEOORN List-serv., 2006). Well-cleaned artificial nest boxes have worked in Peru (Brightsmith 2001), but not in Costa Rica (pers. obs. 2007).

If artificial nest boxes are placed close together or near natural cavities, macaw territoriality may leave empty cavities, an invitation for bees or a raptor (Tut, pers. comm. 2006). In Belize, a Barred Forest-falcon was seen nesting in a cavity in a tree next to an active Scarlet Macaw nest (Britt 2010c). The macaw nest was poached, but any chicks in that nest would probably have been predated by a falcon in such close proximity. Unused cavities near known nests should be closed, perhaps boarded up, to prevent bees or raptors from making nests close to a Scarlet Macaw cavity.

Physical checking of nest cavities should occur mostly after the chicks have hatched; in Peru, frequently monitoring of nests during incubation has meant fewer hatchings of *Ara m. m.* (Brightsmith & Vigo-Trauco 2010). Some nest monitoring could be done by remote camera or video, allowing visuals of predation, poaching, and fledging, as is being done in Guatemala (WCS-Guatemala & Wildlands Security 2008; Ponce et al. 2009) and Costa Rica (Arias et al. 2010). Some of the cameras are solar-powered. Cameras could be placed unobtrusively in the nest or focused on the nest cavity from nearby trees. External cameras might be a target for poachers, but if several camera boxes are installed per nest, with only one having a camera, the odds are higher that a poacher will climb and find an empty box. Nest monitoring, as currently practiced by FCD in the Macal and Raspaculo, may satisfy the requirements of the environmental mitigation paid for by Belize Electricity Company Limited (BECOL), but data are unavailable because of a confidentiality agreement. Despite some value in the monitoring because FCD guards nests as they monitor, data cannot be shared with outside sources to gather assistance in FCD's efforts to help Scarlet Macaws.

MACAW EDUCATION PROGRAMS

Environmental education about Scarlet Macaws was active in the village of Red Bank after 1997, when a macaw shooting was publicized, but as of June 2009 there had been no recent environmental education programs there. FCD is headquartered far away, but some conservation organization should have a regular presence in Red Bank. Although Red Bank is just outside the Toledo district, the Toledo Institute for Development and Environment (TIDE) could serve that function in Red Bank. Most of its villagers are of Maya or Ketchi descent and much of TIDE's work is with villages similar to Red Bank.

Some of the basic natural history of the Scarlet Macaw in Belize and the conservation challenges it faces should be presented by FCD, perhaps in a PowerPoint presentation, and posted with other information on the FCD website.

Outside Belize, there are macaw education programs for the Great Green Macaw in Costa Rica (Arias et al. 2009; Figueroa et al. 2009); the Blue and Gold Macaw (*Ara ararauna*) in Trinidad; the Military Macaw (*Ara militaris*) in Mexico (Macedo 2009; Magallon et al. 2009; Rubio et al. 2009); and the Scarlet Macaw in Peru (Brightsmith 2002), in Costa Rica (Araujo 1998; Dear et al. 2005a), and in Guatemala (Durán de Benítez & León 2004). An excellent overview of general educational techniques and strategies is *Conservation Education and Outreach Techniques* (Jacobson et al. 2006). Excellent resources from Mexico that could be translated into English and adapted for Belize are a downloadable *Kit para maestros sobre pericos* (Teacher's Kit About Parrots) (Cantu et al. 2009) and a Scarlet Macaw poster (Mendez 2009), *Conoces a los pericos: libro para colorear* (Know the Parrots: a Coloring Book) (Sanchez & Mendez 2009). From Guatemala, *La Guacamaya Roja: libro para colorear* (The Scarlet Macaw: a Coloring Book) (Tut et al. 2005) is available.

COMMUNITY ECOTOURISM/INCOME PROJECTS

Red Bank would benefit from an annual Macaw festival, held in February, to highlight the visiting Scarlet Macaws and provide an opportunity for more tourists to come to the village with their ecodollars. Similar festivals organized for macaws in Mexico (Macedo 2009) and Costa Rica (Arias et al. 2009) have been quite successful. These festivals featured talks on bird conservation, children's drawings and crafts, a photography exhibition, bird-watching events, awards to conservation project volunteers, workshops about ecotourism, dance groups, plays, and national publicity. Guided walks to see Scarlet Macaws, environmental education talks, along with cultural events and crafts could all be a part of a Scarlet Macaw festival at Red Bank. If the Belize Tourism Board promoted it, as they do the Cashew Festival near Crooked Tree Wildlife Sanctuary, it would put Red Bank on the tourist map and provide economic incentive to care for all the natural resources of the area, including macaws.

Red Bank has the potential to be the best, and best known, Scarlet Macaw watching spot in Belize. Other good spots exist along the Macal River in the Chalillo Reservoir, but they are far from paved roads, whereas Red Bank is just a few miles off the modern Southern Highway and near the tourist town of Placencia. The potential seen by Programme for Belize, which set up a Macaw Group and procured funding for a guesthouse at Red Bank (Romero 2004), still exists. In Peru a number of lodges and local communities benefit from flocks of parrots and macaws eating clay along local rivers (Munn et al. 1991; Brightsmith 2002, 2007; Brightsmith et al. 2008). Income from those lodges provides jobs for locals and money for research as well, which could happen at Red Bank too, if only seasonally.

Research at Red Bank could be done year-round by either paid interns or volunteers. In Mexico, several villages participated in conservation work on the Military Macaw (*Ara militaris*) and were paid by the government for their assistance (Rubio et al. 2009). Even if the Belizean government cannot devote funds for such research, grants might be found for daily point counts, tree-planting nurseries, fire watches, and patrolling - all done for very little money by trained locals.

Key to any such progress at Red Bank will be local leadership on behalf of Scarlet Macaws and conservation in general. Some leadership does exist, but much volunteer time and energy are required to get the Macaw Group reorganized, a Macaw Festival started, and the Guesthouse program running again. One possibility would be to ask for a Peace Corps volunteer or an equivalent person, who would have the time and education to assist the native leadership in making progress for both people and macaws in Red Bank. Future work could be informed by several articles relating specifically to ecotourism and macaws (Vaughan & Liske 1991; Munn 1992; Talbot & Gould 1997; Munn 1998; Brightsmith 2002; Brightsmith et al. 2008).