ALL OF YOUR EGGS IN ONE BASKET: CONSERVATION OF A MICROENDEMIC ENDANGERED SPECIES

by

LESLIE EILEEN RUYLE

(Under the Direction of John C. Maerz)

ABSTRACT

Effective conservation of endangered wildlife requires a multi-disciplinary understanding of issues. Ecological knowledge of species combined with the effects of human activities on those species should be applied when developing conservation programs. Conservation efforts need to be evaluated for their effectiveness in meeting both ecological and social requirements for protection of species and impacts on local human populations. My dissertation sought to contribute to conservation efforts of Central America iguanas by using traditional ecological studies for foundational knowledge of a critically endangered species, *Ctenosaura melanosterna,* and examining the impact of humans living with that species. Additionally, I evaluated iguana farming as a conservation strategy meant to benefit local populations as well as protect iguanas. Specifically, I examined four different sites of varying degrees of human activities and the impact of those activities on *C. melanosterna* in regards to tick loads, tail loss frequency, behavior and density. Tick loads were correlated to ctenosaur density and tail loss frequency was correlated to presence of domestic animals. Behaviors changed to be bolder with human presence and densities of ctenosaurs were highest at sites with humans, but no domestic animals. We found human impacts depend on availability of food subsidies as well as presence of domestic animals. We provide a study on the growth and survival of *C. melanosterna* that will serve as a baseline for the species in monitoring programs. We also conducted a population viability analysis that suggested the species may be in decline despite conservation protection. Finally, we evaluate a conservation strategy aimed at providing alternative income, an inexpensive protein source, and alleviation of hunting pressures on wild iguanid populations. We found little evidence that this strategy is meeting any of the proposed goals and may in fact be detrimental to conservation goals. We argue that farms may actually work against conservation by encouraging animals to be sold into the pet trade, and possibly putting wild populations in danger from release of farm animals that may carry parasites or disease because they were brought in as stock from other areas or as a consequence of farming practices.

INDEX WORDS: Black chested Spiny-tailed Iguana, Jamo, *Ctenosaura melanosterna*, Population dynamics, Mark-recapture, Program MARK, Population estimation, Life history, Lizards, Reptiles, Iguanas, Ctenosaurs, Farming, Conservation

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CHAPTER ONE

INTRODUCTION

The global growth of designated protected areas (West et al. 2006) combined with an exponentially increasing human population has created a dilemma for conservation practitioners. This is characterized in two ways: first, human settlements near protected areas are subject to expansion, placing greater demands on both resources inside the protected area as well as pressure for the land in the protected area. Second, lands newly deemed valuable for conservation may include areas where human settlements already exist. Thus, protected areas may be threatened both by encroaching populations as well as by pre-existing human settlements (Wittemyer et al. 2008). An on-going debate within the global conservation community vacillates between exclusionary policies (where humans should not be allowed to live in or harvest from protected areas) and social science based management programs (that emphasize humans as part of the protected area) as to the most effective and equitable strategy for management (Agrawal and Redford 2006; Brockington et al. 2006; McShane et al. 2011; Roe 2008; Wells and McShane 2004; Wilkie et al. 2006; Wilshusen et al. 2002).

Proponents of community-based natural resource management (CBNRM) find the paradigm of removing people to create “pristine” reserves to be largely inefficacious and may even attract more settlements to those areas (Wittemyer et al. 2008). Displacing people to create reserves have in some instances reduced the amount of land available for farming or to support livestock, limited access to water, or prevented people from collecting wood and herbal medicines from within the protected areas (Ghimire and Pimbert 1997). In some instances, people's access to areas of spiritual significance have been restricted (Mason and Danso 1995). Social scientists argue that such limitations often create antagonistic feelings towards protected areas and the target species for conservation. This in turn can undermine conservation efforts that protected areas are intended to support (Agrawal and Ostrom 2001; van Schaik and Kramer 1997; Wilshusen et al. 2002).

Integrated conservation and development projects (ICDPs) include community-based natural resource management programs (CBNRMs) and are anchored on the premise that stakeholders in protected areas can better conserve species when they are included in the management plan because local people have a greater interest in the sustainable use of natural resources and better knowledge of local ecological processes (Brosius et al. 1998; Redford and Stearman 1993). For well-designed programs, protected areas may provide benefits to local residents in the form of ecosystem services or revenues from eco-tourism. In the 1990s, conservation organizations hoping to mitigate the negative effects of conservation on the well-being of people increasingly advocated for the policy of inclusion of native populations in protected areas (Brosius et al. 1998; Sheppard et al. 2010). However, the potential for negative effects of human activities on threatened and endangered species has led some biologists to vociferously advocate for the exclusion of people from conservation areas (Kramer and van Schaik 1997; Oates 1999; Terborgh 1999; Terborgh and Peres 2002). Realistically, human settlements are already a pervasive and rapidly increasing presence within and proximate to most protected areas (Wittemyer et al. 2008), so management of conservation areas requires the integration of both biological and social concerns.

The potential impact of humans on species of conservation concern may be particularly acute for island species already more vulnerable to extinction. Island endemics are more prone to extinction because they occupy small areas of habitat with few opportunities for recolonization. The list of cases where human activities have dramatically impacted island endemic species is long. Two of the more prominent examples of island ecosystems impacted by humans are Mauritius and the Galápagos Islands. Mauritius, famous for the now extinct dodo (*Raphus cuculattus*), also lost almost half (46%) of all its reptile species, including the endemic Mauritian Giant Skink (*Leiolopisma mauritiana*) due to human activities (Arnold 1980; Hume 2006). The Galapágos archipelago, an internationally known protected area with human settlements, has domestic animals originally introduced by humans, which resulted in dramatic habitat alterations. Herbivores such as goats, pigs and donkeys have had severe impacts on the vegetation, especially as they went feral and were able to outcompete many of the native endemics including several tortoise species (*Chelonoidis* spp.) and land iguanas (*Conolophus subcristatus)*. Additionally, dogs and cats are non-native predators of adult and juvenile iguanas and birds while pigs often root up nests and consume their eggs. These examples provide evidence that most human activities may be incompatible with conservation of island endemics, and that more stringent management plans are needed for endangered species living in protected areas on islands.

However, in addition to concerns for native people, it is also important to understand how human populations affect the very endangered species that these lands are created to protect. Human trophic subsidies in the form of food waste, edible non-native plant species, availability to fresh water, and additional hibernacula could perturb natural trophic webs (Jessop et al. 2012).

The Black-chested Spiny-tailed Iguana, Ctenosaura melanosterna, as a model system

Ctenosaurs, or Spiny-tailed Iguanas, are a genus in the family Iguanidae, subfamily Iguaninae, that includes 18 species with limited distributions throughout Mexico and Central America. Of the 18 species, 12 are listed as endangered or critically endangered (IUCN 2012). *Ctenosaura melanosterna* (Fig. 1) is one of the species listed as critically endangered by the IUCN (2012). A Honduran endemic, *C. melanosterna* is found in only two areas of the country; one in the Rio Aguán Valley of the mainland and the other on the Cayos Cochinos Archipelago off the northern coast of the country (Fig. 2). A recent molecular phylogeographic study recommends that the mainland population and island populations be considered two different evolutionarily significant units (ESUs) (Pasachnik et al. 2011). We will briefly review human impacts on mainland ctenosaurs; however, the focus of our empirical work was to evaluate whether human activities are affecting *C. melanosterna* island populations.

The mainland population and the island population of *C. melanosterna* differ in several critical attributes. The mainland population lives in the Rio Aguán Valley in scrubby forests dominated by *Acacia riparia*, *Opuntia* sp., *Stenocereus* sp. (Cactacea) and *Hematoxylum brasileto* (Hume 2006). The island populations of *C. melanosterna* occupy more lush, evergreen oak forests. On the mainland, *C. melanosterna* is economically valued as a protein source and medicinal food (L. Ruyle pers. obs.). In fact, the ctenosaur is so highly prized as a culinary item on the mainland that there is an annual “Jamo Festival” [Jamo is the local term for the ctenosaur] in Olanchito celebrating the consumption of the lizard. Gravid females are particularly popular for use in the local cuisine for both their meat and eggs. Nearby Pico Bonito National Park protects habitat for this lizard and an endemic Honduran Emerald Hummingbird, *Amazilia luciae*, but enforcement of hunting regulations is lax (Pasachnik et al. 2011). Habitat loss and absence of true protection in conservation areas, compounded by specific hunting pressures on gravid females, create a serious long-term survival conservation concerns for this species on the mainland. In contrast, the Garifuna People of the Cayos Cochinos Archipelago do not have a tradition of eating *C. melanosterna*; therefore, the island populations face less hunting pressures than the mainland populations. The chief of the archipelago's natural resource patrol force, Elias Aguilar, believes it is possible that ctenosaurs are hunted on the island for sale on the mainland (E. Aguilar pers. comm.); however, while we have observed on several occasions poachers taking green iguanas (*Iguana.iguana*), we never observed anyone taking *C. melanosterna* (L. Ruyle pers. obs.). Therefore, poaching to sustain mainland consumption does not appear to be a major current threat to the island *C. melanosterna* populations.

The Protected Area

In 1993 the Cayos Cochinos Archipelago, a set of two islands and thirteen coral cays located approximately 17 kilometers off the northern coast of Honduras, was designated a marine protected area. Although, the area was described as protected, a management plan was not formalized until 2003 (Brondo and Bown 2011). The protection of the area is the responsibility of the Honduran Coral Reef Foundation (HCRF). HCRF is a Honduran non-profit organization created by several prominent business leaders from the area in cooperation with a Swiss conservation organization, AVINA, interested in the conservation of the archipelago. HCRF, in conjunction with other conservation organizations including The Nature Conservancy (TNC) and World Wildlife Fund (WWF), created a management plan (HCRF/TNC 2008) for the protection of the archipelago. Several of the islands are owned by individuals or by groups of private stakeholders that are expected to adhere to the rules and regulations created by HCRF.

The People

The Cayos Cochinos Archipelago has been home to the afro-indigenous Garifuna people since 1797 (Brondo and Bown 2011). The Garifuna are descendants of runaway African slaves that live along the coast of Central America, of which the largest population (approximately 250,000 people) inhabits Honduras (Brondo and Bown 2011). Traditionally, they have survived as artisanal fishermen using two permanent settlements in the Cayos Cochinos Archipelago: Chachahuate of the eponymous island, and East End on Cayo Mayor. Today, the majority of people of living in the Cayos Cochinos Archipelago are subsistence fishers with some members of the community supplementing their incomes by catering to tourists with food, lodging, or artisanal crafts. With the creation of the Cayos Cochinos Marine Protected Area, the Garifuna were allowed to continue living and fishing in the area but given various restrictions regarding natural resource use. These restrictions limited harvesting of plants, as well as terrestrial and marine life. The islands residents include a small population of expatriates (foreigners) that either own or lease property either on the big island (Mayor) or one of the islands in the archipelago. The majority of these people are seasonal residents although a few live there year round.

To date, few studies have examined the conservation of endangered species through multiple biological and social lenses. My dissertation takes an integrative, multidisciplinary approach towards the conservation of a geographically limited and critically endangered reptile by generating a comprehensive understanding from the biological and socio-economic perspectives. My research integrates population ecology with human influence on populations, and evaluates an iguana conservation model. Although my dissertation focuses particularly on iguanas, the approach is one that can be applied to a variety of endangered species.

In Chapter 2 of my dissertation we present a case study of a critically endangered spiny-tailed iguana, *C. melanosterna*, living in the protected area of the Cayos Cochinos Archipelago, Honduras, to illustrate the effects varying human pressures on an endangered species. We use a three-year mark-recapture study to detect differences in parasite load, tail loss frequency, behavior, and population density at four sites within the archipelago. Our results shed light on how human presence may affect ctenosaur populations and provides information to conservation managers seeking to create use policies in a protected area. In Chapter 3, we perform an in-depth population ecology study of *C. melanosterna* to determine body size, growth rates, age, and age structure. We use program MARK (White and Burnham 1999) to estimate annual survival and capture probabilities, population size, and population growth rates. Finally, we use these data to evaluate population persistence using Monte Carlo simulations in a population viability analysis (PVA). Our results provide the first in-depth population study for this critically endangered species and set a foundation for further monitoring of the population. For Chapter 4, we explore the evolution of iguana farming as a means of conservation in Central America. Specifically, we visit farms and conduct interviews to determine the efficacy of the farms in respect to their goals of poverty alleviation, protein production, and relieving pressures on wild populations. Our results suggest that iguana farms not only are not meeting their desired expectations, but that their efforts may be counter-productive to conservation.

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CHAPTER TWO

BEHAVIORAL AND ECOLOGICAL DIFFERENCES OF ENDANGERED CTENOSAURA MELANOSTERNA POPULATIONS IN RELATION TO HUMAN ACTIVITY[1]

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ABSTRACT

Threatened or endangered species living in protected areas alongside human settlements pose a different set of conservation challenges relative to those occurring in exclusion zones. Human activities may influence directly and indirectly the characteristics of populations that co-occur with humans by affecting factors such as higher rates of mortality and injury, shifts in behavior, and use of novel habitats and food resources which may alter demographic rates and life histories compared to populations in exclusion zones. The Black-chested Spiny-tailed Iguana (*Ctenosaura melanosterna*) is a critically endangered lizard inhabiting a protected archipelago off the northern coast of Honduras. We sampled *C. melanosterna* at four sites over three years consisting of 832 captures of 656 individuals among four sites to describe the relationship between human activity and variation in parasite load, frequency of broken tails, behavior, and density. High levels of human activity including domestic animals and trophic subsidies (food waste, water, and refuges) characterized two of the sites. Two of the sites had low levels of human activity and no domestic animals, although one provided trophic subsidies. Tick loads were not clearly associated with human density or activity, and were instead positively associated with ctenosaur density. Ctenosaurs had a higher frequency of broken tails in areas of high human density with the presence of domestic animals. Larger ctenosaurs and ctenosaurs in areas of high human density fled in closer proximity and shorter distances when investigators approached, suggesting that ctenosaur boldness increases with age and human density. Ctenosaur density was greatest at the site with high human density (food subsidies) and no domestic animals. Ctenosaur density was lowest where there was both high human density along with domestic animals. Our results show that human activities are affecting ctenosaur populations, but

the effects are context dependent. Our work suggests subsidies in the form of garbage promote bolder behavior by ctenosaurs, however, the presence of domestic animals results in higher injury rates and ultimately a lower density of lizards. Management plans for *C. melanosterna* should account for patterns of human habitation and activity on the archipelago.

INTRODUCTION

There is growing consensus that conservation cannot depend on the use of exclusion areas set aside for threatened or endangered species. For most species, there is simply insufficient area to sustain a large number of populations in the relative absence of humans. Reliance on exclusion areas concentrates conservation into a few, small areas that are vulnerable to stochastic loss. Displacing humans to expand or create additional exclusion areas can generate conflicts, and in some cases cultivate a culture of poaching or malicious killing that may ultimately undercut conservation efforts. Ways to maximize the compatibility of human activities with wildlife conservation will reduce the impact of conservation on humans and lead to more effective conservation. This will require an understanding of whether and how human activities affect the characteristics of endangered populations.

Known effects of human activities on species in conservation areas include changes in demography, behavior, and health indices. Reduced survivorship and declining population growth rates occur in populations of the Allen Cays Rock Iguana (*Cycluran cychlura inornata*) at sites that receive higher levels of human visitation compared to those with less impact (Iverson et al. 2006). Impala (*Aepycerus melampus*) populations outside protected areas in Tanzania had lower densities, female biased sex ratios, and longer flight initiation distances than populations found inside the National Park (Setsaas et al. 2007). Parasite loads were higher and body condition indices lower in the common wall lizard (*Podarcis muralis*) at sites with human impacts (Amo et al. 2006).

The effect of human activities on protected species within conservation areas is often related to human density and the nature of human activities. Human activities can alter habitat use. In cases where human activities result in higher mortality (e.g., hunting, poaching, or harassment by domesticated animals), animals may avoid those areas resulting in areas of human activity supporting smaller densities of animals (Setsaas et al. 2007). Conversely, human activities can create novel habitats and food subsidies in the form of trash, which may result in high occurrences of animals within areas of high human activity (Guyer 1988, Hines 2011, Jessop et al. 2012). Human activities can also alter disease and parasite dynamics of wildlife, which contribute additional threats to the conservation of wildlife (Daszak et al. 2001). Humans and domestic animals can expose animal populations to novel parasites or pathogens. Human effects on the environment can alter disease transmission rates through effects on animal density and distribution, and directly (e.g., application of pesticides) or indirectly (increase stress levels) affect immuno-competence of animals. Finally, a number of studies and reviews have noted that understanding human effects on animal behaviors are critical for conservation management. Human effects on behaviors include altered mating behavior, song repertoires, social structure, and boldness (Berger et al. 2007; Bonnaud et al. 2011; Iverson 1978; Rodl et al. 2006; Stone and Snell 1994).

Human activities affect boldness of non-human animals. Boldness is a propensity to engage in risky behaviors such as inspection of novel environments or objects, to use areas of high risk, or to resist flight behaviors in the presence of potential risks (Amo et al. 2006). Boldness is a negative predictor of survival in captive reared and released animals (Bremner-Harrison 2004), and animals may act shier in areas where humans hunt them (Aastrup 2000, Altmann 1958). Increased boldness is also regularly associated with a tolerance of human activities. Many successful invaders and species that occur in close proximity exhibit greater boldness than conspecifics or species that are unsuccessful invaders (Cote et al. 2010a, Rehage and Sih 2004). Boldness may be related to increased tolerance of stresses associated with human activities (Scales et al. 2011), or be related to the ability to exploit novel habitats (Coleman and Wilson 1998, Cote et al. 2010b) and resources that humans provide such as food subsidies (Réale et al. 2007, Scales et al. Wilson et al. 1994).

The genus *Ctenosaura* has 18 species with limited distributions among the arid regions of Mexico and Central America. Twelve of these species are listed from vulnerable to critically endangered on the Red Data Book of the World Conservation Union (IUCN 2012). *Ctenosaura melanosterna* is a medium sized, spiny-tailed iguana whose geographic distribution is restricted to two small areas in Honduras, one on the mainland of the Rio Aguán Valley and the other on the Cayos Cochinos Archipelago. Previously biologists considered the Honduran population as a conspecific of *Ctenosaura palearis* until Buckley and Axtell (1997) described it as a separate species based on morphological data. Recently, the mainland and insular populations were divided into two separate Evolutionary Significant Units (ESU) (Pasachnik et al. 2011). The IUCN Red List Assessment lists both the insular and mainland populations as Critically Endangered due to limited geographic ranges, habitat destruction, and over hunting (IUCN 2012). The insular population of *C. melanosterna* is restricted to the Cayos Cochinos archipelago off of the north coast of Honduras. Cayo Cochino Menor, a small island with an area of 65 hectares, lacks development except for a 2 ha permanent facility for the archipelago's management station. There are no permanent residents on the island, however the number of HCRF staff/visitors fluctuates between approximately 5 to 130 people. Cayos Cochinos Menor functions as an exclusionary area; however, as a single small island it is vulnerable as a conservation asset for *C. melanosterna*. *C. melanosterna* occur on three additional islands in the archipelago; however, humans also inhabit the islands. Understanding the effects of human activities on *C. melanosterna* populations is important in evaluating the potential for these islands to contribute to the conservation of the species.

Our objectives were to evaluate parasite loads, the frequency of broken tails, behavior, and population density of *C. melanosterna* in relation to human activities. Previous studies have used these same metrics to evaluate the impact of human activities on lizard populations (Amo et al. 2006; Hines 2011; Iverson et al. 2006; Lacy and Martins 2003). We examined four locations characterized as no human activity, human activity [food and water subsidies] without domestic animals, and high human activity with domestic animals. Other studies have found that human activity is associated with increased parasite loads of lizards (Amo et al. 2006, Semeniuk et al. 2009); therefore, we predicted that tick loads on *C. melanosterna* would be higher in areas of human activity. Assuming that lizards would be most stressed in areas of high human activity with domestic animals, we predicted that tick loads would be highest in that area. Dogs and cats are predators of iguanas (Berger et al. 2007; Iverson 1978). *C. melanosterna*, like most members of Iguaninae, use tail autotomy as an antipredator adaptation (Arnold 1988); therefore, we hypothesized that the frequency of tail loss would be greatest in the area of high human activity with domestic animals. Variation in population structure reflects differences in recruitment, survival and growth among sites. Humans create, passively or actively, subsidized food resources; however, the presence of domestic animals increases risk and is known to increase shyness in other iguana species (Stone and Snell 1994). Therefore, we predicted *C. melanosterna* to be bolder [flee at shorter distances] in the area of human activity without domestic animals, but to be shier in the area of human activity with domestic dogs. Finally, because of the presence of food subsidies, we predicted that *C. melanosterna* are most abundant in the area of high human activity without domestic animals; however, we expect the lowest abundance of *C. melanosterna* in the area of high human activity with domestic animals.

METHODS

Study sites

The Cayos Cochinos Archipelago (Hog Islands) is situated approximately 17 kilometers from the mainland of Honduras and made up of two large rock islands and thirteen small keys (Wilson and Cruz Diaz 1993). We established study sites on three islands in Cayos Cochinos (Fig.1). Although ctenosaurs occupy four of the islands, we were not allowed access to one of the privately owned islands. We sampled lizards at four sites from the remaining three islands: Cayo Menor, Cayo Mayor, and Cayo Chachahuate. We partitioned Cayo Menor into two study sites: Cayo Menor- Populated (Menor P) and Cayo Menor Non-Populated (Menor NP) (Fig. 2).

***Study site 1*- Cayo Menor-Populated (Menor P)**

Menor P is a two-hectare area surrounding the research camp located on the southern tip of the island (Fig. 2). There are no permanent residents on the island; although ~130 people occupy the area around the station between June and August. 3-10 people usually remain on the island between September and February. We estimated that 20 people – usually visiting researchers are on the island between March and May. Visitors to the island are typically monitoring marine turtles nesting or coral reef health, and the research station serves as an intermediate destination for tourists to register visits and watch a short video about the archipelago. In recent years, reality television shows have used this location, creating spikes in human activities around the research station at differing months. Because the majority of the research and activity at HCRF is marine-oriented, few people venture to the interior of the island.

The area around the station is mostly of beach, sloping scrub forest, and housing structures. There is a substantial water catchment system set up in this area as well as dumped food waste. *C. melanosterna* often scavenge around the trashcans and kitchen area. Between 1970 and 1990, a plot of cultivated fruit trees established near the station (A. Solis pers. comm.). Ctenosaurs in the study area use both trees and buildings for refugia.

***Study site 2*- Cayo Menor Non-Populated (Menor NP)**

Menor NP comprises the remaining 63 hectares of the island (Fig. 2). We failed to capture any individual ctenosaurs in either the human populated and non-populated areas of the island, indicating the two areas function as relatively discrete subpopulations. The area is 140 meters at its highest point. A steep ridge runs from the highest point out to the northern edge of the island, another less prominent ridge runs from close to the center point out west, and three beach areas constitute the rest of the island. The forest is approximately 50% evergreen forest with *Quercus* cf. *oleoides* (Fagaceae) making up 90% of the canopy trees (Bermingham et al. 1998). Hollows in the older oak trees are common refugia for ctenosaurs in that area. The vegetation varies dramatically from east side of the northern ridge to the west side, due to prevailing winds. The windward side has very sparse understory; however, the leeward side of the ridge is lush with many dense understory shrubs including *Calliandra* (Fabaceae-Mimosoid), *Connarus* (Connaraceae), *Alibertia edulis* (Rubiceae), *Cupania* (Sapindaceae), and *Ouratea* (Ochnaceae) (Bermingham et al. 1998). There are no permanent structures on this part of the island except for an antenna at the highest point.

***Study site 3*- Cayo Mayor**

Cayo Mayor is the largest island with an area of 165 hectares (Bermingham et al. 1998; Wilson and Cruz Diaz 1993). There is a single, small fishing village, East End, consisting of approximately 22-90 residents and 19-22 homes (Brondo and Bown 2011; HCRF/TNC 2008). On the west side of the island is the Plantation Beach Resort, a small twelve-room SCUBA diving shop, on 4 hectares of land. There are sixteen privately owned homes on the island with mostly seasonal occupants. The habitat structure and vegetation is similar to Cayo Menor. We counted 42 dogs and 4 cats on the island, which predate of iguanas and disturb nesting behavior of females (Hayes et al. 2004; Iverson 1978). There is a limited amount of supplemental food and water available around the sparse human habitation on this island.

Study site 4- Chachahuate

Chachahuate is the smallest of the study islands with an area of approximately two hectares and the most densely populated with a maximum population of 200 people and average resident population of 90 people in 43-56 houses (Brondo and Bown 2011; HCRF/TNC 2008). Inhabitants of Chachahuate work as fishers or cater lodging and meals to tourists. Fishers from the mainland use the island as a base for fishing. Six dogs and three cats are on the island. There are very few natural resources on this island, with the majority of the island covered by homes interspersed with coconut palms (*Cocos nucifera*). There are two small, unidentified hardwood trees on the island. The authors have observed ctenosaurs eating human waste off the beaches and scavenging from trash heaps.

FIELD METHODS

Lizard capture

We collected lizards from each site using a variety of methods: handheld noose, traps, and by hand. We measured snout-vent length (SVL to the nearest mm), tail length (TL to the nearest mm), and broken tail re-growth (BTL to the nearest mm) of each captured animal. We systematically examined and recorded the number of ticks on the head, dewlap, skin pockets in the axilla, post-femoral areas, cloaca, tail, and toes. We determined sex using external secondary sex characteristics including enlarged femoral pores, tail width, head size. We uniquely identified lizards using two methods: (1) we injected passive integrated transponder tags (PIT) subcutaneously into the left ventral abdominal wall to provide a permanent number for identifying animals over time, and (2) we painted unique numbers on each side of the animal with Wite-Out® to identify recently captured animals. The second mark allowed for the rapid identification of recently captured individuals, which reduced handling time.

Behavior

We used flight initiation distance (FID) and distance fled (DF) to compare boldness differences among lizards at each of the four study sites. We define FID as the distance between the observer and the ctenosaur when the animal first flees from the observer's approach following Cooper et al. (2007). We define DF as the distance the ctenosaur flees from the initial location to the first location stopped after the flight is terminated. We conducted our approach trials between 1000 h and 1500 h during the peak of lizard activity. To ensure that we did not count individuals more than once, we used a combination of unique identification, either through dewlap markers or painted numbers on their sides, and we moved in only one direction through the study site. We slowly (40m/ min) approached lizards to record FID and DF.

Line Transect Estimation of Density

We used line transect sampling (Buckland et al. 2001) to estimate relative densities of *C. melanosterna* among the four sites. At each site we established three 100 meter transects that represented overall habitat diversity. We used three transects because our smallest site, Chachahuate, is so narrow that it could only accommodate three 100 meter transects. We referenced the start and end point of each transect with a Garmin GPSmap 60CSx unit. We characterized the vegetation every 10 meters on each transect as: 1= beach, 2= low vegetation of less than 50% cover, 3= high vegetation of greater than 50% cover, 4= forest with low density understory of less than 50% cover, and 5= forest with high density understory of greater than 50% cover. We recorded temperature, cloud cover, and survey start and end times. We surveyed each site on four consecutive days starting at 1000h. Our sampling period coincided with peak ctenosaur activity. During a survey, we slowly walked each transect and observed ether ctenosaurs or movements in the foliage suggestive of the presence of ctenosaurs. For every ctenosaur we observed, we then used a laser rangefinder to mark the first observed distance in meters of each animal from the transect line and a compass to determine the angle from the transect line. We also measured the perpendicular distance in meters of the first observed distance of the ctenosaur from the transect line as a back up data point. Additionally, we recorded the sex and type of vegetative class (1-5) in which we found each ctenosaur.

Statistical analyses

Tick load

We used a Poisson regression to compare ectoparasite loads among lizards using site and sex as factors to test the hypotheses that tick loads were highest in areas of human activity, and highest in the area of human activity with domesticated animals. Because tick loads could vary among individuals as a consequence of body size, we included SVL as a covariate. We conducted our analysis using a Poisson regression within a generalized linear model in JMP (JMP® 2010) with a Poisson distribution for the error term and a log-link function.

Proportion of population with tail loss

We compared tail break frequencies within and between the sexes and among islands. We separated males and females because male-male combat can often result in injuries including tail loss. We used a contingency analysis to compare the frequency of broken tails at first capture between the sexes and among sites.

Behavior

To test the predictions that flight initiation distances (FID) and the distance fled were shorter for ctenosaurs in areas of human activity without domestic animals, and longer in areas of human activity with domestic animals, we used one-way ANOVAs with site as our main factor and FID or DF as our dependent variable. We used post-hoc Tukey tests for pair-wise comparisons among sites.

Density

We used program Distance 6.0 (Release 2.0) (Thomas et al. 2010) to calculate a relative density estimate for the four sites. We established a global detection function from distance data pooled across the geographical strata due to low detections at some of the sites. However, because habitat cover differed between geographic strata (proportions of beach, low understory, high understory, low understory in forest, and high understory in forest), we assumed this might have an influence on detection probability among strata, so we incorporated these vegetation categories as a covariate in our analysis. Thus, the global detection function is scaled for each habitat type, so we could calculate more accurate estimates of detection probabilities and hence density for each stratum. We used an information theoretic criterion for model selection using the lowest Akaike's Information Criterion and appropriate biological suitability to select the best supported model.

RESULTS

We captured 656 animals, sometimes repeatedly for a total of 832 captures from 2008-2010, primarily in the months of March through July and in all months of the year with the exception of December, February and one day of January (Tables 1 and 2). We captured lizards with noose poles (70.1%), followed by traps (21.7%), or by hand (6.7%). We found 1.1% of our captures dead and recovered 0.4% of ctenosaurs from boas, other ctenosaurs, or dogs. We outline in Table 3 summary statistics regarding sample areas, number of humans, adventitious availability of resource subsidies, and number of dogs and cats per site. Resource subsidies were available from Chachahuate and Menor P, while dogs and cats were at Mayor and Chachahuate. The highest site for human density per hectare was Chachahuate (100/ha) followed by Menor P (65/ha, although seasonal), Mayor (0.6/ha), and then Menor NP (0/ha).

Parasite load

Tick load varied among islands and between sexes ($\chi^2 = 34.39$ df = 3, $p < 0.001$; Fig. 4). The number of ticks per individual increased with an increase in body size (SVL: $\chi2 = 43.55$ df = 1, $p < 0.001$). Ticks were absent from any of the lizards captured from Chachahuate.

Proportion of the population with tail breaks

We found no difference between the sexes in the proportion of the population with tail breaks (χ^2=1.98, df=1, P=0.16; Fig. 5); however, there was a difference in frequency of broken tails among sites. As hypothesized, ctenosaurs on Chachahuate had the highest proportion of the population with broken tails (χ^2=16.8, df=3, P=0.001; Fig. 5).

Behavior

We conducted 105 trials across the four sites for the wariness tests of flight initiation distances (FID) and distances fled (DF). Flight initiation distances varied significantly among the sites ($F_{3,167}$=18.8; $p < 0.001$; Fig. 6). Individuals on Chachahuate (2.43 ± 2.2m) had the shortest FIDs and differed significantly from those on Menor P (5.0 ± 1.2) and Menor NP (14.3 ± 1.28) (all *p*-values ≤0.005, from post-hoc contrasts). Individuals on Menor NP and Mayor (9.35 ± 5.6 m) had the longest FIDs and differed significantly from those on all other islands (*p*-values ≤0.001). Mayor and Menor NP were not significantly different.

Flight distances varied among islands ($F_{3,84} = 20.9$, $p < 0.001$), but not sexes ($F_{1,84} = 0.63$, p = 0.43). Adults on Mayor (7.03 ± 2.25m) and Menor NP (6.96 ± 0.51m) had the greatest distances fled whereas Chachahuate (1.01 ± 0.89m) and Menor P (1.92 ± 0.53m) had the shortest distance fled. A Tukey HSD test showed Mayor and Menor NP did not differ and Chachahuate and Menor P did not differ, but the two pairs differed significantly.

Densities

We conducted all line transects for density measurements between 22 May and 12 June 2010. We tested both hazard and half normal functions and found half normal to be the better fit, likely due to the heterogeneity of the geographic strata within each transect line. Density was highest in Menor P with a 62 individual/ ha, more than seven times larger than estimates from Menor NP (8/ha), Chachahuate (5/ha), and lowest in Mayor (4/ha) (Table 4). Menor P was the only site statistically different from the other sites.

DISCUSSION

The results suggest that *C. melanosterna* can persist in protected areas alongside humans; however, human activities may have some negative effects. The results suggest that *C. melanosterna* in areas of human activity are bolder, probably as a response to the availability of food subsidies in the form of garbage and fruit trees. In areas where human activities include the presence of domestic animals (dogs and cats), increased boldness may lead to high rates of attack, as indicated by the high rates of tail loss on Chachahuate and smaller populations. In the absence of domestic animals, access to food subsidies appears associated with higher ctenosaur densities, which was in turn associated with higher ectoparasite loads. Higher parasite loads related to increased host density effects occur in other iguanids (Wikelski 1999).

Collectively these results reveal the complexity with which human activities can influence wildlife. Other studies suggest that the presence of domestic dogs reduces boldness of iguanids (Stone and Snell 1994, Rodl et al. 2006); however, we found the opposite pattern. We attribute this to the availability of food subsidies. The combination of food subsidies but increased predation risk from domestic animals appears to result in lower lizard densities, which leads paradoxically to the positive effect of low parasite loads. In contrast, the presence of food subsidies without pressure from human hunting or domestic predators results in higher lizard densities but consequently high parasite loads. It is important to note that we are assuming relationships are related to food subsidies, and that greater ectoparasite loads would negatively affect ctenosaur performance. We did not find ticks at the Chachahuate site. It is possible that either the founding animals did not arrive with ticks, or that there is a density dependent effect for ticks and the ctenosaur population is not large enough to support the ectoparasites.

Two factors may be responsible for tail breaks in lizards. First, lizards may lose tails as a consequence of an unsuccessful predation attempt (Arnold 1988). Second, male ctenosaurs may lose tails during male-male combat (Corl et al. 2010; Tinkle and Woodward). Tail autotomy is most often representative of survival of an encounter with a predator (Bateman and Fleming 2009; Downes and Shine 2001; Harris 1989). Hence, autotomy may predict predation risk among sites (Chapple and Swain 2004; Cooper et al. 2004; Medel et al. 1988). That said, it is important to acknowledge that tail loss can result from other interactions such as intraspecific fighting, and that tail autotomy can be related to body condition such that differences among populations can be the result of differences in resource availability rather than or in addition to differences in predation risk (Bateman and Fleming 2009; Fox and McCoy 2000). We are assuming that differences in tail loss rates among our study areas were the result of differential predation risk. We found no difference in tail loss rates between males and females. Because males fight more, if tail loss rates were related to intraspecific aggression, we would have expected to see male bias in the frequency of tail loss. Further, we would expect tail loss rates to have been highest at the sites with the highest ctenosaur densities. Instead, tail loss rates were highest where ctenosaur density was lowest and, as predicted, domestic animals were present and relatively abundant. A remarkable 90% of ctenosaurs on Chachahuate had broken tails. Dogs and cats prey on iguanas of all age classes (Berger et al. 2007; Iverson 1978). Snakes, particularly *Boa constrictor*, are the dominant native predators of adult ctenosaurs, but were absent from Chachahuate. Collectively, these patterns indicate strongly that the presence of humans and their domestic animals increases injury and presumably mortality rates of ctenosaurs.

The results from the behavior trials show that human presence affect flight initiation distance and the distance lizards fled. Ctenosaurs had the longest flight initiation distance on Menor NP, the least human occupied site, but the lowest flight initiation distance on Chachahuate, the site with the greatest human densities. These findings are contrary to other studies that demonstrated animals were less bold around humans and non-native predators (Aastrup 2000; Altmann; Setsaas et al 2007; Stone and Snell 1994). Burger and Gochfeld (1990) and Hines (2011) found that ctenosaurs habituate to human exposure. Our results strongly indicate selection for and/or induction of facultatively bold behavior, i.e., the reward of supplemental food around humans is greater than the risk from domestic animals.

The *C. melanosterna* populations of the Cayos Cochinos Archipelago are an ESU of a critically endangered species living on only a few islands in a hurricane prone area. As a result, dependence on the small island of Mayor as a conservation exclusion area is inherently risky. The populations that occupy additional islands with more intense human activity provide opportunities for distributing the risk to *C. melanosterna*; however, it is clear that those human activities will affect ctenosaurs including reducing densities or increasing parasite loads depending on the nature of human activity. It may be possible to address these specific effects and increase the compatibility of human activities with ctenosaur conservation.

Conservation strategies that blend the use of exclusion zones with management within human-dominated landscapes may be the only way for conservation to truly be successful. As human populations expand, collisions of endangered species with human settlements are inevitable. Compromise is required of both social and biological interests. Different species respond to human presence in a variety of ways and conservation practitioners should take into account how focal endangered species will react to varying human presence pressures when creating management plans.

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Table 2.1. Capture dates for *C. melanosterna* among the four study sites in the Cayos Cochinos Marine Protected Area for the three-year study period.

Year	Captures/ resights/ recaptures	Dates
2008	416	1 Jan, 14 Mar -21Aug, 16 Oct-7 Nov
2009	316	18 Mar -5 Oct
2010	382	21 May- 27 Jul

Table 2.2. Number of male, female, and young of year *C. melanosterna* individuals at first capture among the four sites in the Cayos Cochinos Archipelago.

Site	Males	Females	Young of year	Total
Menor P	130	187	137	454
Menor NP	39	26	40	105
Mayor	14	16	32	62
Chacha	7	11	17	35
Total	190	240	226	656

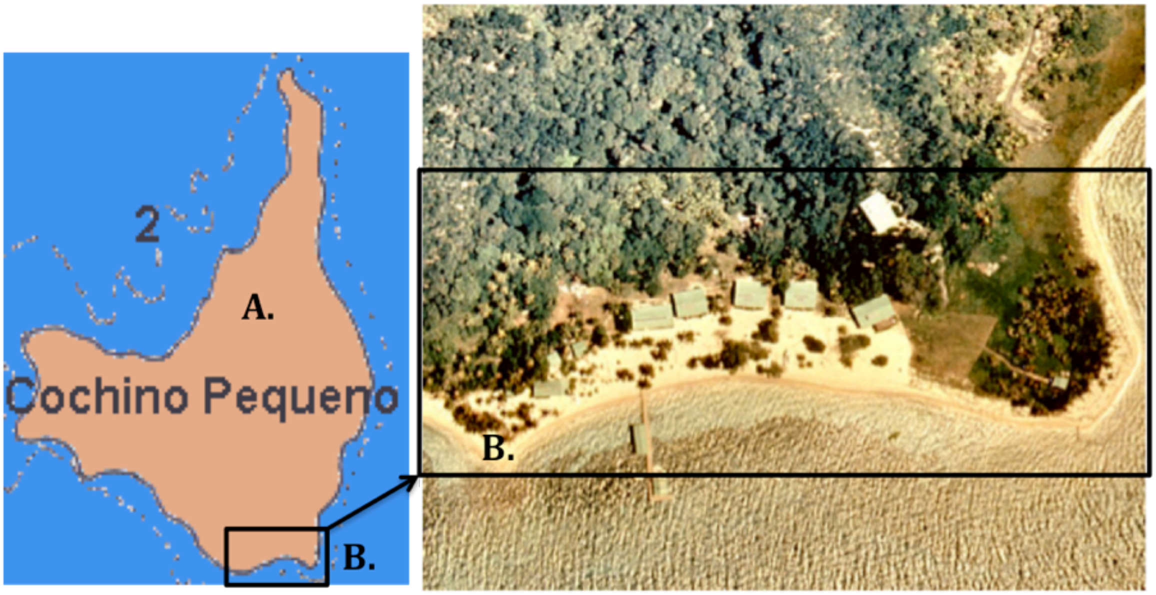
Table 2.3. Summary statistics of sample area, estimated human population, availability of resource subsidies, and presence of dogs and cats. Menor P = Cayo Menor Populated and Menor NP = Cayo Menor – Non-Populated. Sampled area is the area at each island site where transects were established. Human population estimates for Mayor and Menor are based on data from HCRF (E. Aguilar, pers.com.) and from Brondo and Bown (2011) for Chachahuate.

Site	Sampled area (ha)/ (total area in ha)	Human Population Size	Adventitious availability of food/water	# of dogs	# of cats
Menor P	2 (63)	5-130	Yes	0	0
Menor NP	61 (63)	0	No	0	0
Chachahuate	2 (2)	90-200	Yes	6	3
Mayor	73 (153)	22-90	Minimal	42	4

Table 2.4. Summary of the results from Program Distance. Each island is calculated for density of *C. melanosterna* per hectare (D) and per area sampled (N).

Site		Estimate	% C.V.	df	95% CI
Chachahuate	D	4.75	63.16	2.03	0.41- 55.39
	N	9.00	63.16	2.03	1.00- 111.00
Mayor	D	3.95	43.94	2.07	0.68- 22.86
	N	293.00	43.94	2.07	51.00 -1691.00
Menor-NP	D	7.51	34.96	2.10	1.86- 30.27
	N	541.00	34.96	2.10	134.00 - 2180.00
Menor-P	D	61.69	20.14	2.34	29.19-130.36
	N	123.00	20.14	2.34	58.00- 261.00

Figure 2.1. Map of Central America with two inset maps: the lower left corner map shows the Americas while the upper right inset map shows the Cayos Cochinos Archipelago and relative size and location of each of the three islands in the study: Chachahuate, Mayor, and Menor.



A. Menor NP B. Menor P

Figure 2.2. Cayo Cochino Menor (Pequeno) is approximately 63 hectares in area and hosts two study sites: Menor NP (A) and Menor P (B). Menor NP (~61 hectares) encompasses the uninhabited section of the island. B. Menor P (~2 hectares) has a research station situated at the southeastern end of the island and has human activities.

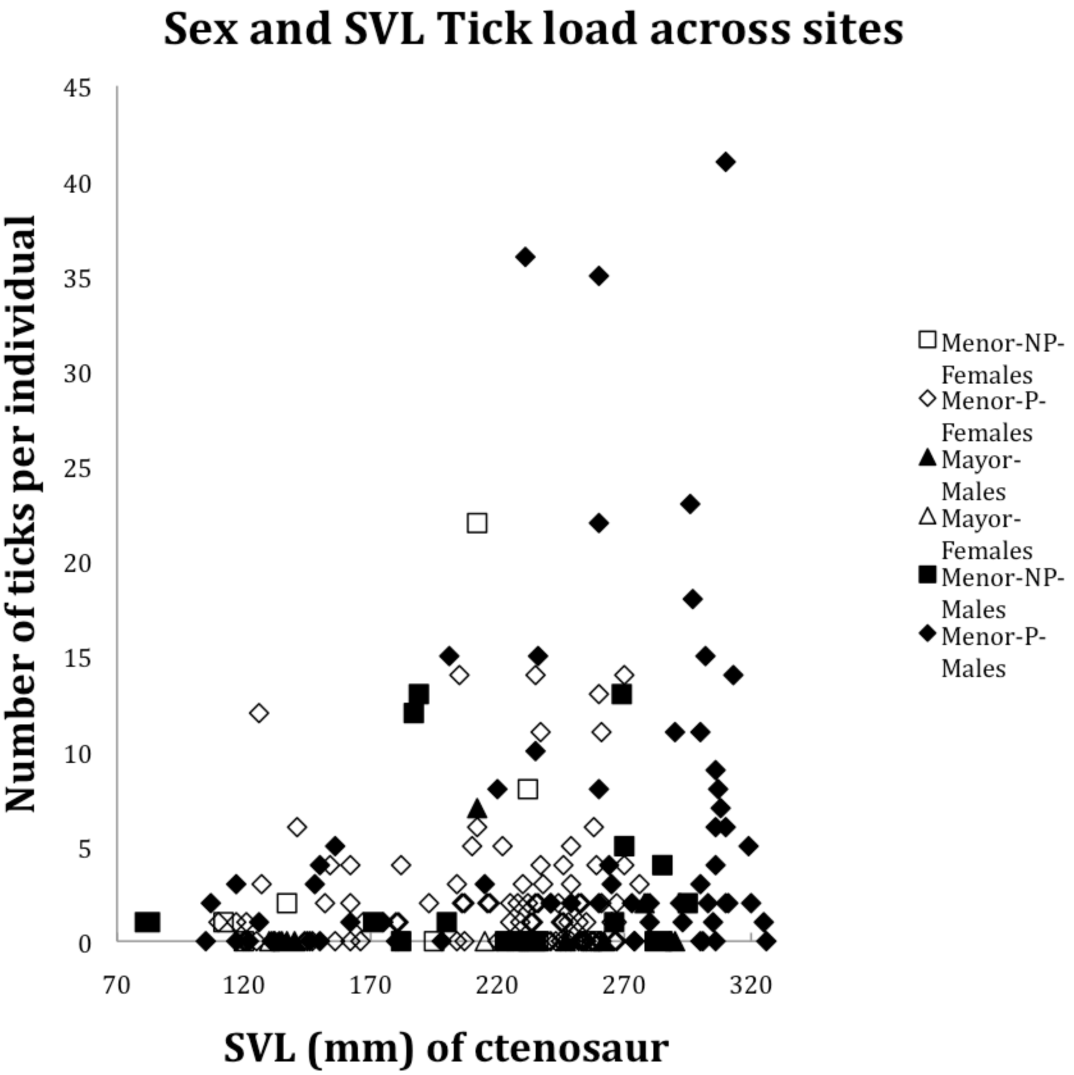


Figure 2.3. Number of ticks per individual by sex plotted against snout-vent length among sites.

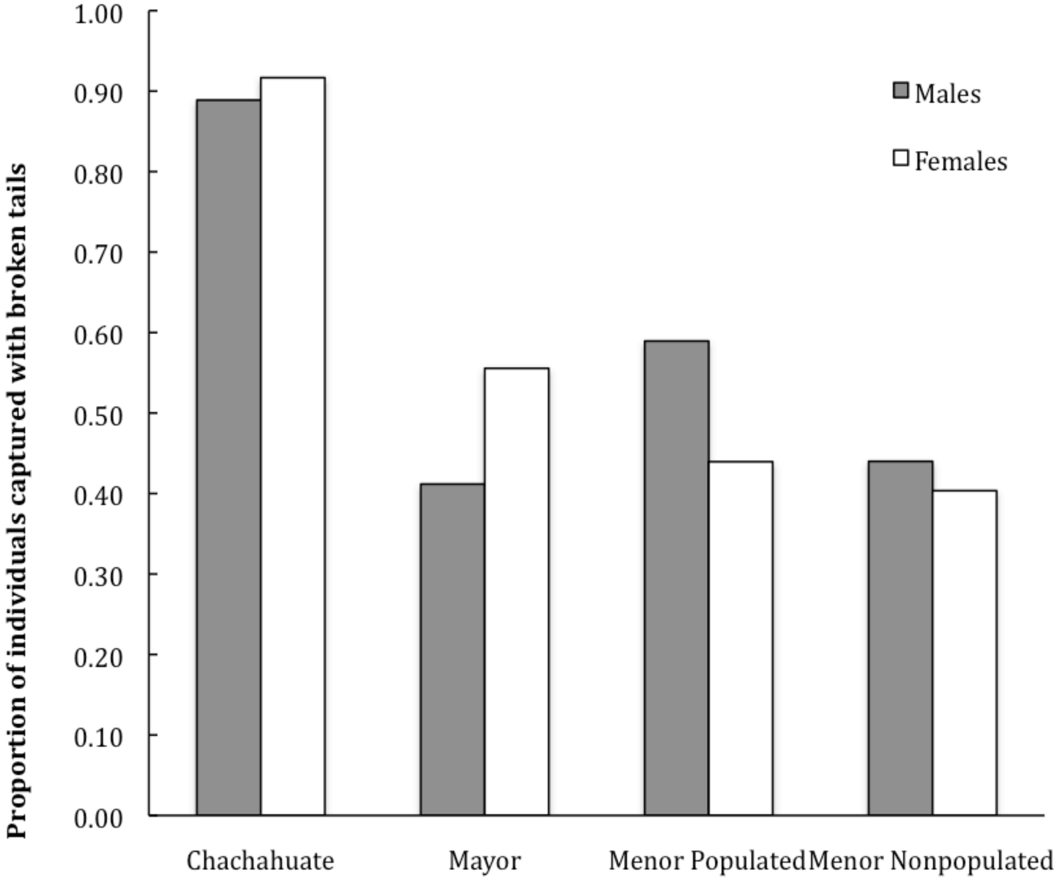


Figure 2.4. Proportion of the population at each site with male (gray bars) and female (white bars) *C. melanosterna* with broken tails.

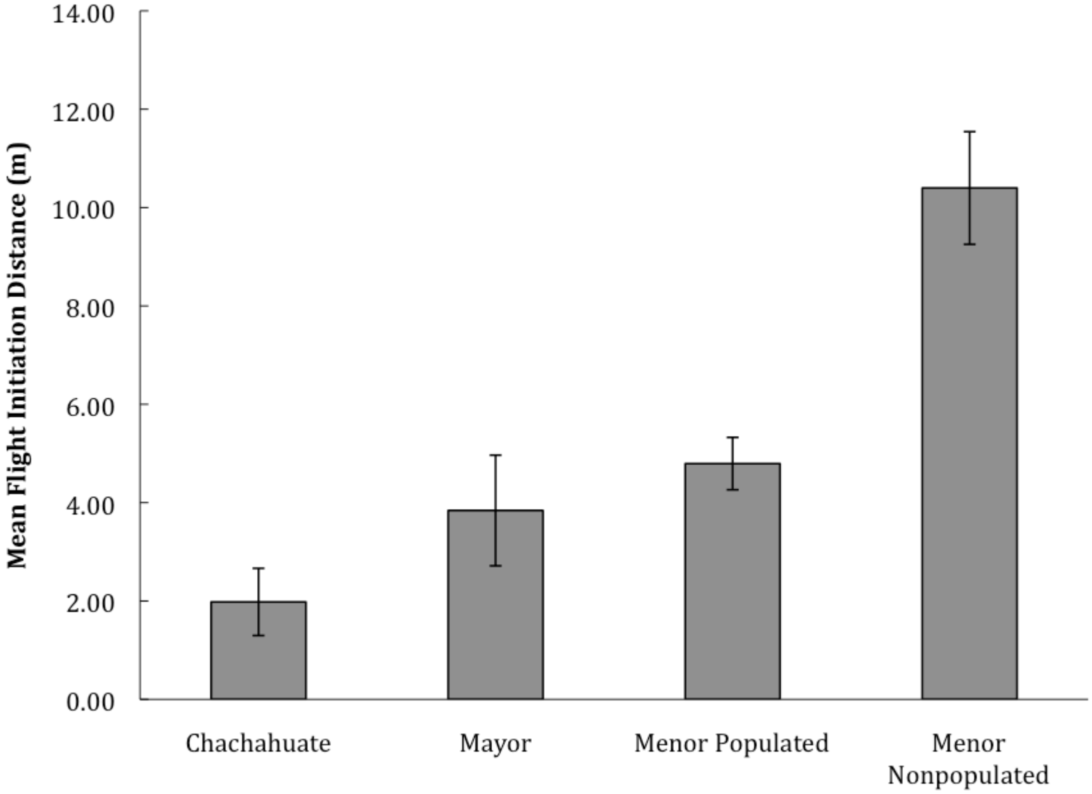


Figure 2.5. Mean flight initiation distance (FID) in meters with error bars of *C. melanosterna* populations among the four sites: Chachahuate, Mayor, Menor Populated (P), and Menor Nonpopulated (NP).

CHAPTER THREE

DEMOGRAPHY, GROWTH, AND SURVIVAL OF THE BLACK-CHESTED SPINY-TAILED IGUANA IN CAYO COCHINO MENOR, HONDURAS

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[2] Ruyle, L., Todd, B., Miles, D., Montgomery, C., and Maerz, J. To be submitted to *Herpetological Conservation and Biology*.

ABSTRACT

Demographic data are essential for building effective conservation management plans. These data are critical, especially for management of small populations of endangered species with restricted distributions that are vulnerable. Here we present data on the life history and demographic patterns of a critically endangered, insular reptile species, *Ctenosaura melanosterna,* based on a four-year capture-mark-recapture study. We estimated body size, growth rates, age, and age structure. In addition, we estimated annual survival and capture probabilities, population size, and population growth rates. Finally we used these data in a Monte Carlo population viability analysis model to assess the susceptibility the species to extinction. We had 747 captures of 454 individually marked ctenosaurs yielding 129 males, 187 females, and 138 young of the year <80mm. We found males to be longer than females and more broadly distributed across size classes than females. Growth rates were higher in males and females. Females appear to attain reproductive size in approximately two years. Males had lower survival rates (73%) than females (94%). Males were approximately twice as easy to catch as females. We estimated the mean population size over the 4 years to be 379 individuals (males 179± 3.8, 95% CI =135.8-152.8; females 240±24.9, 95% CI=208.8-313.1) and obtained an average estimate of λ, the population growth rate, as 0.91 (SE= 0.09; 95% CI= 0.76- 1.11). Our Monte Carlo PVA simulation estimated persistence of the *C. melanosterna* population in 100 years to be 28% but with a population estimation of 2 individuals. Our study reinforces the importance of long-term data for ascertaining the population of a long-lived species to make more accurate predictions.

INTRODUCTION

The management of small populations in small areas is a common portrait of conservation programs. Small populations and populations with highly restricted distributions are particularly vulnerable to extinction, and for species with few small populations, the conservation value of each of these small populations is great. Assessing the vulnerabilities of small populations is essential to management, and the basis for those assessments are demographic and life history data (Benton et al. 2006; Caswell 2001; Metcalf and Samuel 2007; Saether and Bakke 2000). Demographic data are necessary for determining whether and why species may be declining (Dennis et al. 1991; Fujiwara 2007) including age-specific rates that are more sensitive to perturbation (e.g., Iverson et al. 2006). Demographic models can also be used to design effective population recovery and management plans.

Reptiles are becoming increasingly threatened by human activities, yet many species lack sufficient data to evaluate risk of extinction or development recovery plans (Gibbons et al. 2000). For lizards, detailed life history studies are available for many common temperate species (Dunham 1981; Galliard et al. 2010; Sears 2005; Tinkle et al. 1993; Tinkle and Dunham 1983); however, fewer studies have focused on tropical lizard species or on endangered species with small populations (Fry 2001; Guyer 1988; Iverson et al. 2006).

The genus *Ctenosaura* has 18 species with limited distributions among the arid regions of Mexico and Central America. *C. similis* is the lone exception with a large distribution ranging from southeastern Mexico to Central America (Fitch and Henderson 1978). Two species in the genus, *C. bakeri* from Utila, Honduras and *C. oedirhina,* from Roatan, Honduras are exclusively limited to islands. Twelve of these species are listed from vulnerable to critically endangered on the Red Data Book of the World Conservation Union (IUCN 2012). Few studies have addressed the population biology of the genus (Fitch and Henderson 1978; Gutsche and Streich 2009) which are critical data for creating conservation plans. The absence of estimates of key vital rates, recruitment and survival, coupled with limited data on age and size structure of the population, limits the ability to derive estimates of population variability and the persistence of a species.

Here we present data on the life history and demographic patterns of a critically endangered, insular reptile species, *Ctenosaura melanosterna,* based on a long-term capture-mark-recapture study. We estimated body size, growth rates, age, and age structure. In addition, we estimated annual survival and capture probabilities, population size, and population growth rates. Finally, we use these data to evaluate population persistence using Monte Carlo simulations in a population viability analysis (PVA) with the goal of evaluating extinction risk and estimating sensitivity to catastrophic events.

METHODS

Study species

Ctenosaura melanosterna is a medium sized, spiny-tailed iguana whose geographic distribution is restricted to two small areas in Honduras, one on the mainland of the Rio Aguán Valley and the other on the Cayos Cochinos Archipelago. Previously this population was considered to be a conspecific of *Ctenosaura palearis* until Buckley and Axtell (1997) described it as a separate species based on morphological data. Recently, the mainland and insular populations have been divided into two separate Evolutionary Significant Units (ESU)

(Pasachnik et al. 2011). *C. melanosterna* is a sexually dimorphic lizard with adult males having heavier mass, longer snout-vent length (SVL), and broader jowl width. Additionally, males have larger dewlaps, a bluer coloration, and enlarged femoral pores. The lizard is an opportunistic and omnivorous predator. Observed prey items range from foliage, fruit, insects, birds, other conspecifics, and human refuse (L. Ruyle ms in prep). Breeding occurs from March - May and females lay clutches of 7-22 eggs (L. Ruyle pers. obs.). Hatchlings emerge from June-August (L. Ruyle pers. obs.). The IUCN Red List Assessment lists both the insular and mainland populations as Critically Endangered due to limited geographic ranges, habitat destruction, and over hunting (IUCN 2012). Limited data are available regarding the population structure, life history variation, and demography of this species. Our study aims to help provide for this deficit and provide framework for constructing a solid conservation action plan.

Study site

The insular population of *C. melanosterna* is restricted to the Cayos Cochinos archipelago off of the north coast of Honduras. The archipelago is approximately 17 kilometers from the mainland and 30 km south of the largest Bay Island, Roatan (Bermingham et al. 1998) and consists of two large rock islands, Mayor and Menor, and several small cays (Wilson and Cruz Diaz 1993; Wilson and McCranie 2004). We conducted our study on Cayo Cochino Menor, which is the smaller island with an area of 65 hectares. The island measures 1.5 kilometers from north to south and 1.1 kilometers east to west with a highest elevation point of 140m (Bermingham et al. 1998; Wilson and Cruz Diaz 1993) (Fig. 1). Most of the island lacks development, but there is permanent laboratory/housing infrastructure for the archipelago's management station, the Honduran Coral Reef Foundation (HCRF), in a 2 ha area near the coast. There are no permanent residents on the island, however the number of HCRF staff/visitors fluctuates between approximately 5 to 130 people. We focused our capture efforts in the two-hectare area surrounding the research station and facilities. Several permanent buildings include cabins (5), a dry lab, and three scuba related buildings, which the ctenosaurs use as refugia. A kitchen is situated the hill where three meals are prepared daily. Waste from the kitchen is either discarded over the side of the hill or shallowly buried in the forest behind the cabins. There is very little fresh water on the island with the exception of cisterns located at the research station. The study site is comprised mostly of sandy beach, sloping scrub forest, and research and housing infrastructure.

FIELD METHODS

Lizard capture and morphological measurements

We collected lizards using a handheld noose, traps, and by hand. Our sampling effort involved attempting to capture all lizards seen regardless of sex or size. We measured snout-vent length (SVL) to the nearest mm, tail length (TL) to the nearest mm, the length of the regenerated tail, if broken (BTL) to the nearest mm, and body mass (Mass) in grams for each captured animal. We determined sex using external secondary sex characteristics: enlarged femoral pores, tail width, and head size. We could not reliable determine the sex of individuals less than 80mm using external morphology, and we did not use cloacal probing to sex hatchlings for fear of injury; therefore, we categorized these individuals as new recruits of the year. Prior to releasing animals, we injected passive integrated transponder (PIT) tags subcutaneously into the left ventral abdominal wall to provide a unique number for identifying animals over time. Additionally, we painted unique numbers on each side of the animal with Wite-Out® to facilitate identification of recently captured animals.

Size variation and growth rates

We created an SVL size frequency histogram using data from males, females, and young of the year on their first capture for years 2007-2010. We compared the SVL and mass of males to females at first capture.

To obtain growth rates, we generated a database of size at first capture and first recapture for each interval ≥ 30 days, including the SVL of each animal at each capture date and the number of days between the two captures (initial capture and first recapture). We calculated growth rate increments as mm per day and plotted growth rate versus SVL at midpoint of the 2 captures separately for each sex, following Stanford and King (2004).

Age estimation

We estimated the age of each individual based on its length at first capture for all individuals, following the methods of Van Devender (1978). We used the integrated, linear version of the von Bertalanffy growth equation:

$$Age = (\frac{1}{k})\ln(-Ak + k(SVL)) + c \quad (1),$$

We obtained the values for the growth constant (*k*) from the von Bertalanffy growth equation as implemented using SAS NLIN. We used the maximum value of SVL for males and females as our preliminary estimate of *A* and 50mm at hatching for *c*.

To estimate the age at first reproduction for females, we looked at the change in size and mass for females in a short period of time (e.g., during the breeding season) per Fitch and Henderson (1978). We considered females that showed reduction in body mass during the breeding season consistent with oviposition to be reproductively active. The minimum SVL of females was used to generate our estimate of age of first reproduction based on equation 2.

Survivorship and probability of capture

We used Program MARK (White and Burnham 1999) to generate estimates of survival and abundance based on capture-mark-recapture data and the Cormack-Jolly-Seber (CJS) model. We only used reproductively mature animals >185mm and entered data as recaptures only, including sex as a covariate. We also used default options for link functions and variance estimation (Cooch and White 2006). We fit several models to determine the values for survival (Φ) and capture (*p*) parameters. Finally, for survival we evaluated models that included year and sex. We fit a series of CJS models beginning with a saturated model: Sex and time dependence for survival and capture. This model allowed us to evaluate estimates of time-dependent and sex dependent variation in survival (Φ) and capture (*p*) parameters. Model selection was determined by comparing AICc values (Burnham and Anderson 2002).

Estimation of population size and growth rate

We used the POPAN model in Program MARK to estimate population size following the protocol outlined in Cooch and White (2006). We used the estimates of annual population size generated from the Pradel model in MARK to determine the geometric growth rate, lambda (λ) for *C. melanosterna*.

Population viability analysis (PVA)

We used the population size estimates from MARK and values for population growth rates to simulate population dynamics given stochastic variation in the geometric growth rate. These values provided the ability to conduct a PVA to assess the risk of extinction within 100 years (Boyce 1992). Rather than use a population projection matrix approach, we focused on assessing the consequences of stochastic variation in population growth rates on population persistence. Our approach uses a Monte Carlo simulation following the spreadsheets of Donovan and Welden (2002). Other studies have used a Monte Carlo simulation to model extinction risk in lizards and endangered species (Dennis et al. 1991; Fitzgerald 1994). Our model involves predicting population size over time given stochastic variation in the finite rate of increase (λ). The advantage of this approach is the ability to generate multiple repetitions without requiring multiple assumptions regarding population structure, genetic variation and age specific vital rates. We assumed that variation in λ would follow an inverse normal distribution. We used excel to model the change in population size given stochastic variation. We used MARK estimations of initial population size and population growth rate (λ) in a Monte Carlo simulation, with 0.1 as the λ standard deviation (SD). To assess whether the population was viable we used a standard of 95% persistence after 100 years.

RESULTS

We had 747 captures of 454 individually marked ctenosaurs and 249 resights yielding 129 males, 187 females, and 138 young of the year <80mm. To highlight the distribution of size variation in the population, we plotted the SVLs at first capture of males, females, and young of the year (Fig. 2) into eleven size classes of ~24mm increments from 55mm-325mm. Males were more broadly distributed among the size classes than females. Approximately one third of the male population was distributed across three size classes: 251-275mm (9.5%), 276-300mm (11.9%), and 301-325mm (8.7%), while 30% of the female population was in the 226- 250mm size class. Males were significantly longer than females ($F_{1,404} = 110.68$; $P < 0.001$; average male SVL = 272.44 mm ±2.26; average female SVL = 236.47 mm ± 2.41, Fig. 3). The longest observed SVL for males was 322mm, whereas the longest female observed attained a length of 274mm. The majority of hatchling SVLs were between 55-65mm, although some were slightly longer or shorter. When we plotted mass against SVL, we found that males and females generally follow the same growth trajectory, but that males grow larger than females (Fig. 3).

Adult growth rates were higher in males (0.083 mm/d ±0.015) than females (0.047 mm/d ±0.011). Growth rates were also significantly greater in juvenile males (0.19±0.01 mm/d) than females (0.16±0.025 mm/d). We plotted individual instantaneous growth rates for both male and female individuals based on actual capture-mark-recapture (CMR) data (Figs. 4 and 5). As shown in other studies, growth rate decreased as ctenosaurs increased in size, and males exhibited higher instantaneous growth rates than females after adjusting for body size.

We estimated the age of each individual based on its length at first capture for all individuals, following the methods of Van Devender (1978). We used a size of 50 mm at hatching for *c,* and asymptotic size for males (male A= 311.4) and females (A= 270.5) using growth rate (k) =0.00014. (Fig. 6). Based on the fitted age equation we could then estimate the age of all individuals across all years. We then plotted data of individuals to illustrate the age across the population (Fig. 7). The maximum estimated age attained by males is 11 years and females is 10 years. Given the relationship between age and SVL, we find that first reproduction for females is likely between the sizes of 185 - 200mm. When we combine these results with our growth data, it appears that females are capable of attaining reproductive size in approximately two years.

We found the highest supported model included a sex specific term for survival (Φ_s), and a sex and time specific term for capture probability (p_{s*t}). This model had the lowest deviance and highest AICc of all competing models and the highest likelihood support. Survival varied between sexes with males having lower survival than females (Table 4). Females exhibited higher probabilities of survival at 94% (SE=0.09) while males had a lower probability of survival at 73% (SE=0.06). Capture probabilities differed between the sexes and among years (Table 4). Males were approximately twice as easy to catch as females among all years.

Estimated survival probabilities did not differ over time, but they did differ between the sexes (Table 4). We estimated that adult females had a higher survivorship (0.94) than adult males (0.73). The best fitting model included a significant heterogeneity in capture probabilities between the sexes and across sample years (Table 4). Capture probabilities were consistently higher for males (0.36-0.69) than for females (0.12-0.39) and higher than females in each of the three recapture years (Table 1).

We estimated the mean population size over the 4 years to be 379 individuals (males 139± 3.8, 95% CI =135.8-152.8; females 240±24.9, 95% CI=208.8-313.1) and obtained an average estimate of λ, the population growth rate, as 0.91 (SE= 0.09; 95% CI= 0.76- 1.11).

For our initial PVA, we used initial population size of 379 individuals and mean population growth rate (λ) = 0.91 (SD = 0.09). Using the mean estimated λ of 0.91 in our first simulation, we found the mean population size in 100 years of populations was 0.05 individuals (SD =0.87). Our simulation estimated persistence of the *C. melanosterna* population in 100 years to be 28% but with a population estimation of 2 individuals. Given an initial population size of 379 individuals, we evaluated the probability of a decline in abundance given a range of λs between 0.99 and 1.03. Our results yielded 3% chance for the population to be greater than N (t=0) at λ of 0.99, 30% to be greater at λ of 1.00, 72% at 1.01, 87% at 1.015, 92% at 1.02, and 100% at 1.03. Therefore, the population must show a 3% realized rate of population growth rate to maintain a stable population size given the variation in λ (SD= 0.10).

DISCUSSION

The *C. melanosterna* population at the Cayo Cochino Menor research station area is characterized by a female biased population (1:1.4) and individuals may continue to live and grow for up to eleven years. The species exhibits male biased sexual size dimorphism (SSD) which is typical for the genus and most iguanid lizards (Hollingsworth 1998). One third of the female population was in the 225-250mm size class, while adult males were more evenly distributed among the size classes.

The growth increment data show that males grow faster than females. This is consistent with *C. similis* where both juvenile and adult males grew faster than females (Fitch and Henderson 1978). We estimated that *C. melanosterna* females are reproductive at approximately two years of age, consistent with the similarly sized *C. similis* (Fitch and Henderson 1978) and slightly before the smaller *C. bakeri* at 2.5 years **(**Gutsche and Streich 2009).

The annual survivorship estimates of approximately 73% for males and 94% for females of *C. melanosterna* is similar to those found in other long-lived lizards. Iverson demonstrated survivorship estimates of 87% for males and 93% for females in the Allen's Cays Rock Iguanas (*Cyclura cychlura*) (2006) and 95% for males 90% for females in *Cyclura carinata* in the Turks and Caicos Islands (1979). Galapagos marine iguanas (*Amblyrhynchus cristatus)* were estimated to have survivorships of 79% for males and 83% for females (Laurie and Brown 1990).

Similar to the findings of Iverson (2006) and Laurie and Brown (1990), males had a lower survivorship probability than females. Iverson et al. (2006) attributed these differences to male boldness, which they believe may have exposed these iguanas to higher predation pressures (e.g., birds of prey, dogs, cats), harassment by tourists, or poaching. Alternatively, they suggest that aggressive encounters among males during mating season may influence survival rates

(Iverson 2006). At our site, *Boa constrictor* is the primary predator of adult ctenosaurs. Our capture probabilities were consistently higher for males than females supporting the suggestion that males are bolder or easier to capture; however, lizards at this site are not exposed to the suite of predators that are at other sites, making boldness less a factor in predation attempts. High densities of ctenosaurs (~190 ctenosaurs/ hectare) may exacerbate territorial disputes and male-male combat. Males often had intense fights that led to death or loss of limbs, crushed skulls, and broken backs well beyond the high breeding season (L. Ruyle pers. obs.). Male-male conflict may better explain differential sex survival at the research station site.

There are several important limitations to PVAs in general and in our PVA specifically that should be noted. First, PVAs are notoriously difficult models to create that accurately represent population dynamics (Beissinger and McCullough 2002) and often rely on numerous difficult to meet assumptions (Conroy and Carroll 2009). There are several different packaged models designed specifically for small populations (VORTEX (Lacy 1993), WALEX (Possingham and Davies 1995), RAMAS (Akcakaya et al. 1999)) depending on data to be analyzed and desired outcome (Beissinger and Westphal 1998). However, there is criticism that the use of these packages can often be used inappropriately by overreaching the reliability of the data to determine parameter values, and it is recommended that for conservation biologists to better reach their objectives to constructing simple models with transparent assumptions and deficiencies (Conroy and Carroll 2009). We used this advice in choosing our Monte Carlo simulations. Second, our PVA is based on estimates from a four-year CMR study, which for a long-lived species such as *C. melanosterna*, it is difficult to ascertain whether this is truly indicative of the population growth rate trajectory long term. Beissinger and McCullough recommend (2002) at least three years of data collection to estimate a probability of survivorship for a single year. Congdon et al. (1994) stresses that it may be difficult to detect population responses due to long generation times. Our estimates are unlikely to capture 'true' population growth rates because our estimates are based on 4 years, not sufficient for an accurate estimate for a long-lived species. Finally, our PVA does not take into account several key demographic variables including clutch size, hatchling and juvenile survival rates, and a female biased sex ratio.

We found a particularly high population density at this site compared to other insular populations of *C. melanosterna* (L. Ruyle Chapter 1). We suspect high levels of human food subsidies, water, and alternative refuges (buildings) combined with protection from animals associated with human settlement (dogs, cats, chickens) promote a higher density of ctenosaurs compared to other sites (L. Ruyle Chapter 1), which is similar to results found in other studies looking at food subsidy effects (Guyer 1988; Iverson et al. 2006; Jessop et al. 2012). Iguanids are known for their potential of high population growth rates. Documented examples include the escape of an estimated 6-12 Cuban iguanas (*Cyclura nubila*) onto Isla Magueyes off Puerto Rico's coast and growing from an estimated population of 157 adults in approximately twenty years (Christian 1986; Rivero 1978). These results would yield an annual estimate of increase of 14-18%. Even more impressively, between 1988-90 eight subadult Allen Cays iguanas (*Cyclura cychlura inornata*) were introduced to a small cay and grew to a population of 75-90 iguanas by 1998 (Knapp 2001), yielding an annual population growth increase of at least 32% (Iverson et al. 2006).

In contrast to our observations of high relative population densities at this site (L. Ruyle Chapter 1), our calculated population growth rate over the four-year study period was 0.91, indicating a declining population during the period we monitored. Even with high levels of protection and trophic subsidies at this site, our results show that the population is vulnerable with the possibility of extinction at the calculated population growth rate of 29% in a 100- year simulation. Our population growth data are based on only four years of data collection. Our estimation of λ has confidence intervals overlapping a stable population growth rate of 1.0 (CI= 0.76- 1.11), hence it is possible that the population is stable or even growing. We would expect to see fluctuations over the years, and that these effects would be dampened in a long-lived species (Fitzgerald 1994).

It is possible that the research site serves as an ecological trap or population sink for the species. High relative densities compared to other sites in the archipelago (L. Ruyle Chapter 1) may reflect bold animals drawn in for food subsidies. While we do demonstrate high survivorships, 94% for females and 73% for males, our population growth rate (λ= 0.91) shows a declining population. Low population growth rates might be attributed to low recruitment. While we did not measure hatchling survival (recruitment) in this study, hatchling ctenosaurs are vulnerable to a variety of snake species, birds, tarantulas, and conspecifics (L. Ruyle pers. obs.) and the more open habitat at this site could make hatchlings more susceptible to predation. Additionally, high ctenosaur densities may create higher probabilities of intra-specific predation. The authors have observed large numbers of hatchlings depredated by conspecifics and even recorded an incident of a 196mm male consuming a 116mm male. Intra-specific predation has been recorded in other species of iguanas as well (Hayes et al. 2004; Iverson 1979).

An alternative explanation is that the *C. melanosterna* population around the research station serves as a source population to the larger island area. High population densities could be driving less bold individuals into the forest and out of the boundaries of the designated study site;

therefore, making recaptures of these individuals less likely due to both shyness and location resulting in skewed estimates for survival and population growth.

Our paradoxical results suggest that more data are needed to better explain the survival probability of the *C. melanosterna* population at Cayo Cochino Menor. Our estimates of population size or growth rate may be biased due to the limited temporal scope of the study. Additionally, more data on recruitment, hatchling survival, and accounting for adult population sex differences will help refine PVA estimates on subsequent analyses. Our data were limited to the area immediately around the research station; therefore while we feel these data useful in the short term, we recommend that studies further monitor population growth rates on a larger scale both temporally and spatially to fully ascertain the trajectory of the species. Finally, our survival rates were higher in females than males, thus a PVA model that only includes females may provide a higher lambda and thus a more positive outlook for the species at this site.

Demographic data allow biologists to better predict persistence of a species. Populations fluctuate over time, but how demographic stochasticity may influence population dynamics is not known for many long-lived species. These data are critical, especially for island dwelling species where populations are vulnerable to short term stochastic events like hurricanes as well as long term susceptibilities of climate change combined with sea level rise. Species living on low-lying islands are at greater risk to hurricane events that have the potential to wipe out entire populations. Climate change will likely cause sea level rise that may submerge or restrict areas for species living on islands. Our study reinforces the importance of long-term data for ascertaining the population of a long-lived species to make more accurate predictions. The data gathered in these types of studies are invaluable for conservation managers seeking to understand the best methods to protect all species, but with particular urgency, endangered species.

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Table 3.1. Estimates of survival and capture probabilities for *C. melanosterna* on Cayos Cochinos Menor.

Parameter	Sex	95% CI		95% CI
	Males		Females	
Survival	0.73	0.58- 0.84	0.94	0.29- 0.99
Capture				
2007-2008	0.68	0.48- 0.83	0.46	0.31- 0.63
2008-2009	0.36	0.23- 0.51	0.12	0.07-0.21
2009-2010	0.69	0.35- 0.91	0.39	0.22- 0.60

Figure 3.1. Map of Cayo Cochino Menor; the study island in the Cayos Cochinos Archipelago off the north coast of Honduras.

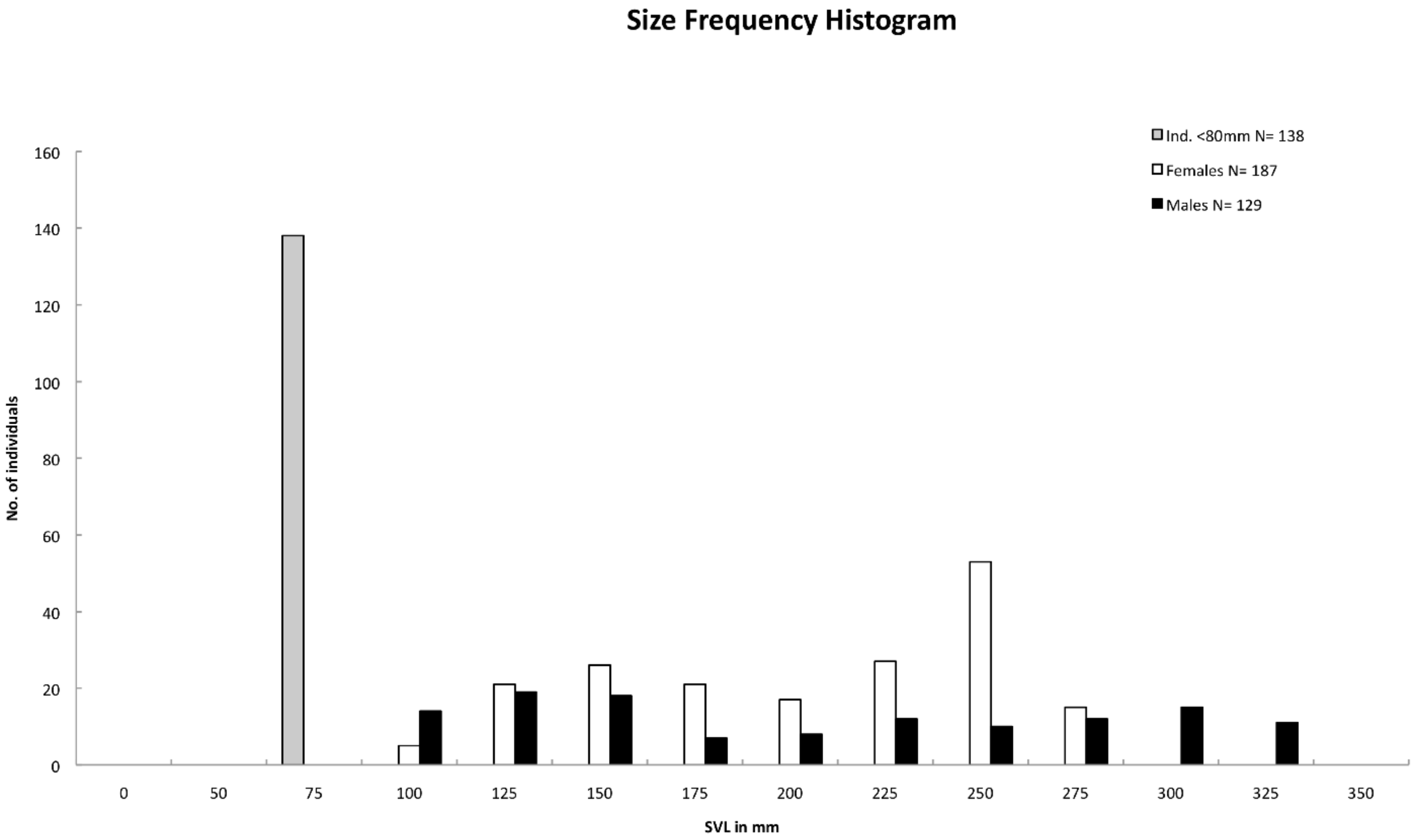

Figure 3.2. Frequency histogram showing the observed number of *C. melanosterna* males (black bars), females (open bars), and young of year <80mm (gray bars) in each snout-vent length (SVL) category at first capture between 2007-2010.

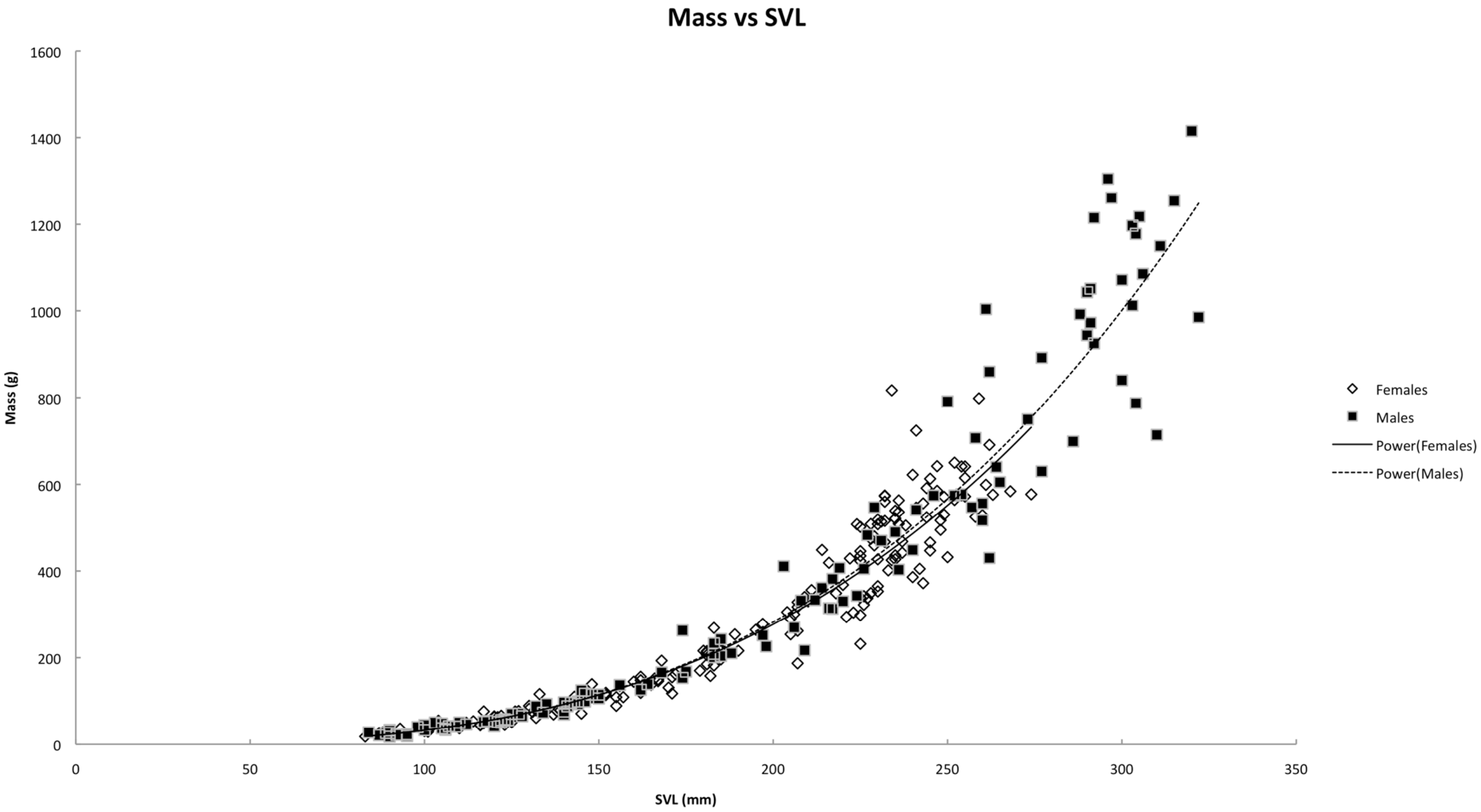

Figure 3.3. Mass versus snout-vent length (SVL) of all first captures of male (black squares) and female (white diamonds) *C. melanosterna* for years 2007-2010. Lizards <80mm at first capture were sexed on recapture and included in the analysis.

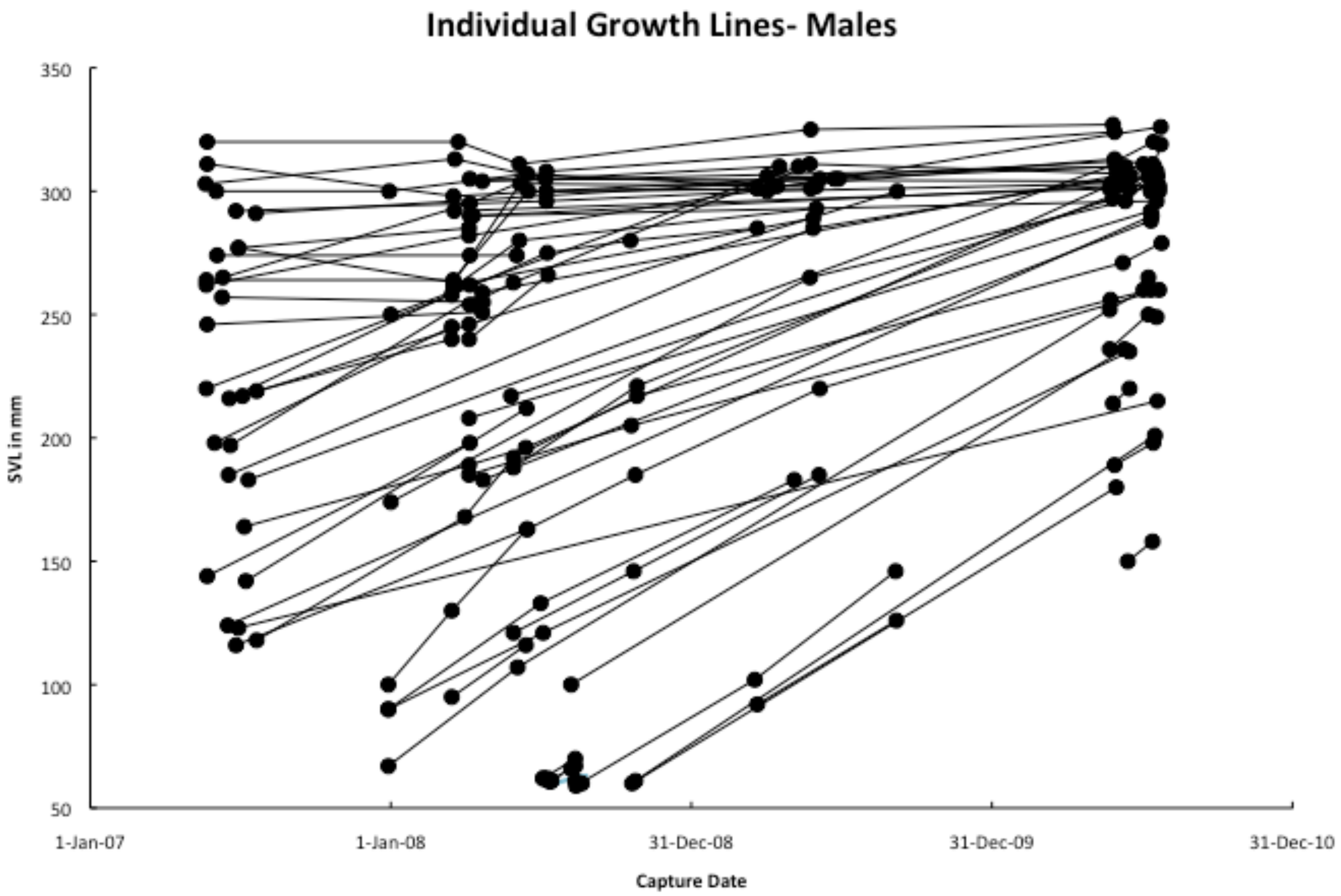

Figure 3.4. Growth lines illustrating individual male *C. melanosterna* snout-vent lengths (mm) at each capture from 2007-2010.

Figure 3.5. Growth lines illustrating individual female *C. melanosterna* snout-vent lengths (mm) at each capture from 2007-2010.

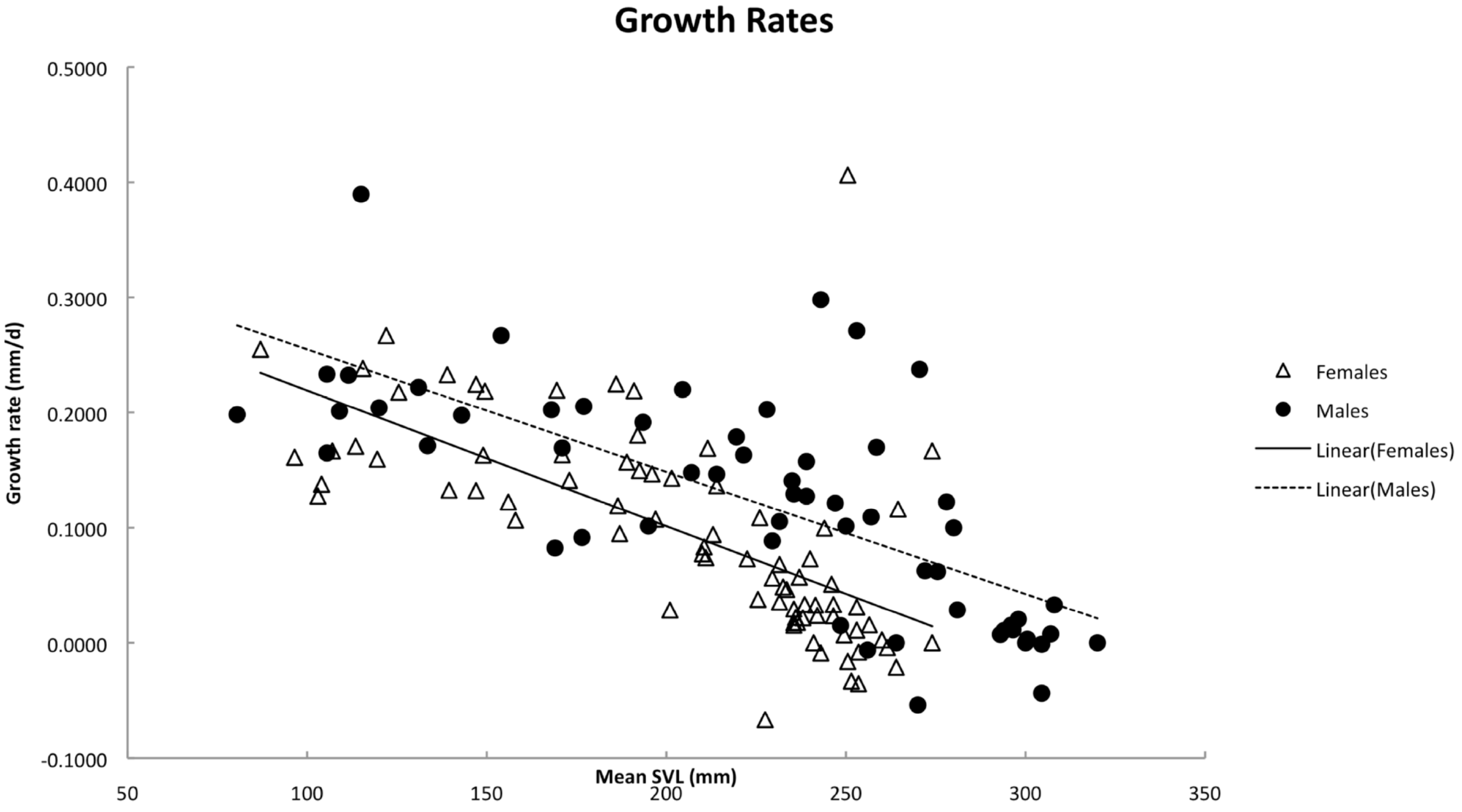

Figure 3.6. Daily growth rate vs. mean snout-vent length (mm) for male (black circles and dotted line) and female (white triangles and solid line) *C. melanosterna.*

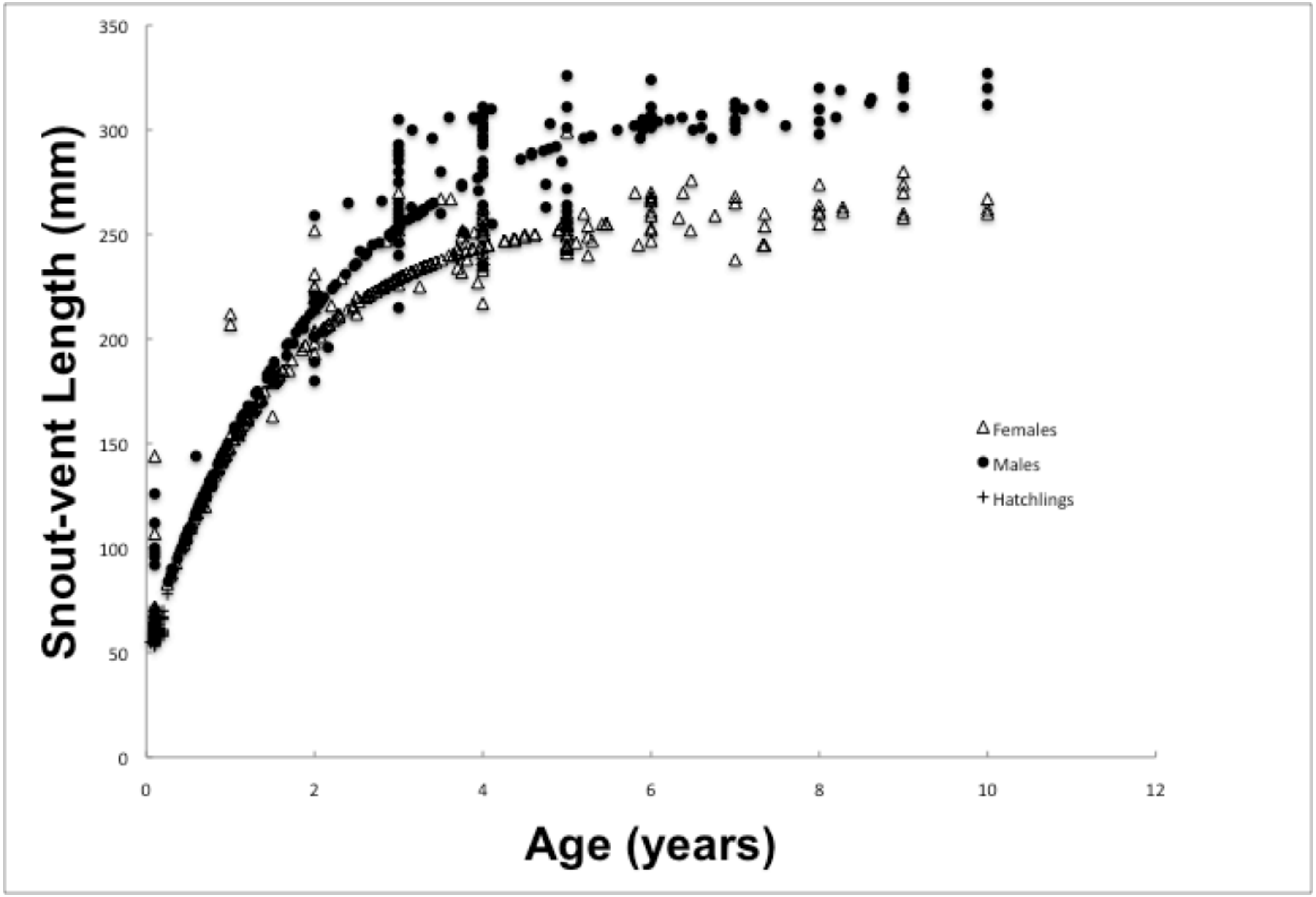

Figure 3.7. Age estimations by year based on snout-vent length for male (black circles) and female (white triangles) *C. melanosterna* for 2007-2010.

CHAPTER FOUR

A CRITICAL EVALUATION OF IGUANA FARMING AS A CONSERVATION STRATEGY[3]

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[3] Ruyle, L., Stephen, C., Fitzgerald, L., and Maerz, J. To be submitted to *Herpetological Conservation and Biology*.

ABSTRACT

Commercial farming of wildlife is a concept popular with conservation organizations hoping to offset threats to species, but little has been done to understand the outcomes for the primary objectives of providing a) an alternative source of income for people that would otherwise harvest animals from the wild, b) sustainable protein source for local communities or c) alleviation of pressures of consumption for wild populations. We examine these questions by visiting facilities and interviewing people farming iguanids in Central America. We document the history of iguana farming and report on the status of farms operating from 20 years to start-ups. Despite the popularity of the concept, we found little evidence that iguana farms are profitable for meat, that any farms sell stock primarily for consumption, or that farms alleviate pressures on iguanids in the wild. We argue that farms may actually work against conservation by encouraging animals to be sold into the pet trade, and possibly putting wild populations in danger from release of farm animals that may carry parasites or disease because they were brought in as stock from other areas or as a consequence of farming practices.

INTRODUCTION

Throughout the world, wildlife products are recognized as an important resource for food, medicine, and skins (Broad et al. 2003). Increasing human populations and improving sources of technology have had large effects on wild populations of hunted species (Bennett and Robinson 2000). Yet, many people in the developing world rely on hunted animals for a cheap source of protein (Dufour 1983; Yost and Kelley 1983), and the bush meat trade is now one of the greatest threats to wildlife (Fa et al. 2002). Conservationists, looking for solutions, have proposed various schemes for eliminating hunting pressures on wild species including creating alternative livelihoods for hunters (Sheppard et al. 2010) and farming or ranching of hunted species (Belsare and Narayankhedkar 2004; Brooks et al. 2010; Nasi et al. 2008; Revol 1995; Rice et al. 1999; Smythe 1991; Thorbjarnarson 1991). Wildlife farms may be a way to develop alternative incomes and provide an inexpensive source of protein, while reducing pressures on hunted populations (Hardouin 1995; Revol 1995; Werner 1991). Reptiles, including turtles (Haitao et al. 2008), crocodilians (Revol 1995), and iguanas (Werner 1989), are good species for testing the relative merits of these alternative possibilities.

Reptile species (including Testudines, Crocodilians, and Squamates) have been a globally important protein source for humans (Klemens and Thorbjarnarson 1995). Humans commonly consume reptiles in the tropics and subtropics where they are most abundant. Turtles are the most heavily exploited reptile group with consumption of both their meat and eggs (Klemens and Thorbjarnarson 1995). Many turtle species including the Pig-nosed Turtle, *Carettochelys insculpta*, (New Guinea); the Madagascan Big-headed turtle, *Erymnochelys* *madagascariensis* (Madagascar); the Central American River Turtle, *Dermatemys mawii* (Central America); and the Red-crowned Roofed Turtle, *Kachuga kachuga* (Indo-Malayan region) are considered endangered due to overexploitation for meat and eggs (Klemens and Thorbjarnarson 1995). Crocodilians are commonly eaten where they occur, though not at the scale of turtle consumption. In South America, Cuvier's dwarf caiman, *Paleosuchus palpebrosus*: the Smooth-fronted caiman, *P. trigonatus;* and the Spectacled caiman, *Caiman crocodilus;* are all small species commonly consumed, whereas in Africa the Dwarf crocodile, *Osteolaemus tetraspis,* is the species most targeted for consumption (Klemens and Thorbjarnarson 1995). In Australia, evidence suggests that aboriginal peoples have exploited crocodile meat and eggs for over 20,000 years (Webb et al. 1987), and crocodiles remain an important local source of protein and commercially important source of hide for making apparel. Among squamate reptiles, species in the subfamily Iguaninae, specifically *Iguana iguana* and *Ctenosaura* spp., have been part of the diet in Central American cultures for over 7,000 years (Cooke 1981). While some groups ascribe medicinal qualities to the meat and/ or eggs (Fitch et al. 1982) others consume iguanas as an additional protein source. Iguana dishes, particularly those with gravid females, are especially popular during Lent, which coincides with breeding season (Fitch et al. 1982).

A common solution presented for mitigating overexploitation of wild populations under threat of hunting pressure is to create farming or ranching opportunities. The goal of these facilities is to enhance the abundance of individuals within a target taxon, so that humans exploit "farm raised" or "ranched" individuals produced in captivity rather than extracting them from the wild. Often these programs are touted as 'win-win situations' by relieving pressures on wild populations from hunting, hence aiding in the conservation of the species, while also producing alternative income and protein sources for local communities (Hardouin 1995).

Current reptile production can be broken down into two categories, farming and ranching, and the distinction between the two practices has economic and conservation implications. Farming involves maintaining stock animals, incubating eggs, and rearing hatchlings to a harvestable size. In contrast, ranching entails either collecting wild eggs or capturing wild, gravid females and allowing them to oviposit in artificial nests. The eggs resulting from these clutches are incubated to hatching and subsequently reared. Both farming and ranching will entail large initial production costs such as construction of housing, artificial nest sites, and rearing enclosures; however farming is likely to have more overhead costs to operate than ranching due to care and maintenance of stock animals. Stock animals need to be kept in good condition to ensure reproductive health (Escobar et al. 2010), which involves suitable habitat, food, and adequate space for social behavior. Because ranching involves collecting animals from the wild in the reproductive season, less space is required for breeding stock. However, there are costs involved in procuring wild animals.

The conservation impacts of farming and ranching depend on the biology of the focal species and that species' status in the area. Ranching may have a greater impact on populations because adults or eggs are collected from the wild. In contrast, farming tends to target the maintenance of brood stock with only initial and limited replenishment from wild populations. Crocodilians are among the best known ranched reptile species in the world (Magnusson 1984). Crocodile ranching began in Zimbabwe in the 1960s and officially authorized in 1966 (Revol 1995), and despite initial appearances of success, failed to deliver on both economic promises and conservation goals (Magnusson 1984). Crocodile farming appears to have been far more rare and abandoned as a practice after early failure.

Iguana iguana **conservation in Central America**

Based on evidence of declines due to habitat destruction and over-harvesting, *Iguana iguana* became one of the first lizard species to have farming and ranching proposed as a conservation tool. The first natural history data on *I. iguana* appeared in peer reviewed literature during the early 1960s (Hirth 1963; Moberly 1964; Rand 1968). Many studies followed making the green iguana one of the best-studied lizard species in the tropics. Based on these baseline studies it became apparent in the 1980s that populations of *I. iguana* had declined due to habitat destruction and over-harvesting. These declines prompted exploration of possible conservation strategies (Burghardt and Rand 1982; Fitch et al. 1982; Werner 1984; Werner 1987). Burghardt and Rand (1982) suggested green iguanas should be considered for ranching due to their high reproductive potential, evidence of captive-raised feasibility (Braunwalder 1979), and sustainability of raising animals over generations (Mendehlson 1980). They questioned whether iguana meat could compete economically as a protein source against other domesticated animals, but alternative sources of economic productivity of green iguanas included specialty foods, pet trade, and laboratory supply animals as supplemental markets (Burghardt and Rand 1982). In the same year, Fitch, Henderson, and Hillis (1982) suggest iguana farming as an alternative to hunting. They also highlighted the difficulty of maintaining profitability competing against other domestically grown animals as well as logistical problems of territoriality and fighting among the iguanas. To counteract economic and space issues, they proposed a compromise of keeping a breeding population of adults while releasing the hatchlings. Potential release sites would be chosen based on the suitability of habitat with a lack of natural populations, and predators would be managed for optimal iguana survival (Fitch et al. 1982).

The widespread implementation of iguana farming in Central America originated from the Green Iguana Management project at the Smithsonian Tropical Research Institute (STRI) in Panama. STRI led a project promoting a program to link iguana conservation, forest protection, and poverty alleviation under one umbrella that could be implemented at the individual family farm level. This model sought to restore wild populations while still allowing for harvest by changing hatching and hatchling survival rates as an augmentation program (Werner 1987). The project used published life history data (Rand 1980) to predict that wild iguanas naturally have a 50% hatching success rate (Harris 1982) and hatchlings have a 5% chance to survive their first year (Van Devender 1982). The project goal was to increase nesting success and hatchling survival rates from a wild 5% to a farmed 95% (Werner 1987) resulting in sufficiently large enough increases in population sizes to allow hunting yet still maintain stable population sizes. The protocol involved local farmers keeping breeding stock, releasing juvenile animals into the nearby forest, while simultaneously providing supplemental feeding stations to increase carrying capacity and keep animals proximate for later harvest. Ideally, local farmers would be encouraged to protect the forest that provided iguana habitat while having a readily available source of protein. Additionally, the project provided farms with brood stock from their facilities that had “enhanced production capabilities” (Werner 1987). The project started in 1983 as the Iguana Management Project, continued as Fundacion Pro Iguana Verde in 1985 and moved to Costa Rica in 1988, where the approach eventually expanded into other Central American countries (Cohn 1989).

Ironically, the rise in husbandry knowledge for iguanas fueled their emergence into the commercial pet trade, and transformed iguana farming and conservation programs. In the 1960s, the first green iguana pet care books were published, and by the 1990s, green iguanas were booming in popularity en route to becoming one of the most recognizable reptile pets in the world. In October 1993, the reptile enthusiast magazine, “Reptiles,” featured a green iguana cover photo on its debut issue. Hatchling iguanas were in high demand, and small-scale farms in Central America were an accessible place for commercial buyers to find them. Selling iguana hatchlings into the pet trade began in El Salvador with small farmers, but larger scale commercial pet farms soon followed. The demand for hatchlings by foreign buyers transformed the original conservation model for keeping iguanas and releasing the hatchlings into the wild. It became much more profitable for farms to sell hatchling iguanas to exporters in the pet trade rather than to release them. NGOs recognized this and soon the conservation model for iguana farming adjusted the protocol from releasing all offspring into the wild into releasing 10-30% of the hatchlings into the wild. In Honduras, iguana farming projects were originally initiated by foreigners and animals transported through El Salvador en route to the global market. Soon the Honduran government and NGOs encouraged farmers to sell hatchlings into the pet trade by providing permits allowing collection and incubation of eggs from wild females. So-called “six-month ranches” proliferated during the iguana market boom years with at least 10 government sponsored farms specifically for the raising of *I. iguana* hatchlings for the pet trade (Gustavo Cruz, UNAH, *pers. comm.*). These local ranches were only in operation six months, which is long enough to produce hatchlings for the pet trade.

With green iguanas now commonplace in the pet industry, their abundance in foreign pet stores may obscure critical evaluation of iguana farming as an economic and conservation tool.

There have been limited efforts to evaluate the current state of iguana farming and ranching relative to the original goals of the program, or to evaluate whether and how iguana farming may serve as a management tool for other iguana species. In this paper we describe current iguana farming activities in Nicaragua, Costa Rica, El Salvador, Honduras, and Guatemala. We evaluate the dissemination of the iguana farming concept and how it has been modified from the original model of iguana conservation to its status today. Finally, we compare the various models of farms currently in operation and their role in iguana conservation across these central Latin America countries. Our aim to is to evaluate whether the iguana farming meets the key objectives of providing a) an alternative source of income for people that would otherwise harvest animals from the wild, b) a source of protein for local communities, or c) alleviating pressures on wild populations. We will argue that farming and ranching have significant flaws as a conservation strategy, and that effort to marry protein production with captive propagation of wild species should consider those flaws in designing and executing a program.

METHODS

From December of 2009 to June 2010, we collected interview data from twenty-one iguana facilities in five Central American countries: Honduras, Guatemala, Costa Rica, Nicaragua, and El Salvador. We contacted NGOs and governmental officials in each country to aid us in selecting appropriate interview participants. We requested information regarding any facility in the country raising any species of Iguanine (i.e., *Iguana iguana*, or *Ctenosaura* spp.). We focused on businesses that raised iguanas for any reason: meat, tourism, or the pet trade. We requested permission from business owners to visit the properties either by ourselves or accompanied by NGO or government officials. We used the snowball sampling method

(Goodman 1961) to expand on this knowledge by asking each person interviewed if they knew of additional farms. We were able to visit 16 farms in three countries: ten in Nicaragua, four in Costa Rica, and two in El Salvador. We collected additional interview data from two farms in Honduras and three farms in Guatemala through email and NGO contact interviews. At each site we interviewed the owner or representative of the farm, using a standard interview sheet. Our interview consisted of three parts: logistics of farm management, maintenance of animal stock, and the economics of operating the farm. Our surveys included questions to collect information measuring profitability, the amount of time and money that a facility requires to operate, whether the facility was a farm or ranch, number of animals sold for meat, and whether the facility released any iguanas. We also describe how the various models of farms described and their role in conservation across Latin America countries.

RESULTS

The facilities that we profiled would best be described by five categories: family-owned farms (14%), community cooperative farms (14%), commercial pet breeding operations (38%), conservation/ tourism breeders (24%), and research facilities (10%). All of the facilities we interviewed farmed *I. iguana*, except for the breeders of *C. quinquecarinata* who collected gravid females from the wild in ranching style while trying to create breeding stock. We found a shift in both how iguana farms were being implemented by NGO and government organizations as well as in how farms operated initially and how they operate today. Several farms that began as a sustainable livelihood meat production projects converted to pet trade suppliers, tourist operations, or closed down.

Economic benefit

We found three possibilities for economic benefit for iguana farms: meat production, pet trade, and as a tourist attraction. 28% of respondents identified themselves as meat production farms, but none demonstrated any profitability and all received NGO funding. Three of the six “meat production” farms had not sold any adults for either meat or breeding stock, nor had they sold any hatchlings into the pet trade since opening. Only one farm reported selling iguanas for meat; a total of twelve males in 2009. We were informed of six local farms that had ceased production due to unprofitability, because we did not speak with their owners, they were not part of our interviews.

Commercial pet breeders comprised 38% of respondents, 87% of which showed a profit, although profits are derived from breeding and sales of a suite of species that include *I. iguana*. The largest and most profitable farm is foreign owned. 100% of the facilities cater to US and European markets, although one start-up hoped to create a more robust local pet trade market in addition to selling internationally. Larger commercial pet breeders reported that previously if hatchling and juvenile orders surpassed their production capacity, they would purchase additional hatchlings from smaller local farms. However lack of current market demand had the largest breeder scaling back on production of *I. iguana* and two other commercial breeders were expected to close soon due to economic concerns.

Twenty- four percent of our surveys (5) came from iguana centers run as tourism enterprises and none reported being profitable. Three operations were converted from meat production or pet breeding farms. Most facilities were now sustained through private donations or international NGO funding.

Protein source

We found 28% of farms identified for iguana meat production, yet only half of those surveyed sold animals. Of those 3 farms, one was selling less than 12 animals per year and the other two estimated even fewer animals sold per year. In our survey 90% of farms raised *I. iguana* and 19% of the farms reared other iguana species, specifically, *C. quinquecarinata, Ctenosaura similis,* and *Ctenosaura bakeri*. *C. quinquecarinata* were raised in two farms, specifically for the pet trade, not for meat. A university was experimentally attempting to create breeding protocols for *C. similis* while a cooperative attempted raising *C. similis*, but was unsuccessful at keeping founder animals alive. *C. bakeri*, an endemic to the island of Utila in Honduras, was bred at one facility and hatchlings all released as a conservation measure. The majority of our interviewees told us there is a higher demand in the meat market for *I. iguana* versus *Ctenosaura* spp. When asked why *C. similis* was not commonly raised in farms, even though we saw the species sold in local markets, we were told that *C. similis* is much more difficult to manage due to their aggressive nature. A large-scale pet breeding operation attempted to create an iguana meat business, but found it to be unprofitable and now gives away surplus males as free meat (name withheld by request, pers. comm.).

Alleviate pressures on wild populations

Fifty seven percent of farms reported releasing animals into the wild. However, there was much discrepancy in this result. The original hatchling release protocol from the Green Iguana Project had been modified from releasing all hatchlings, to 10-30% of clutches, to recent directives from NGOs to not to release any animals. We had conflicting reports as to whether animals were being released, at what percentage they were being released, and how often releases happened.

DISCUSSION

Despite the initial enthusiasm for farming Iguanine species as an alterative source of protein and economic activity as envisaged by conservation organizations, our survey found little evidence that the model is a socioeconomic success, provides a sustainable source for protein, or alleviates hunting pressures on wild iguanas. Revenue for farms were possible through three avenues 1) meat production, 2) pet trade, and/ or 3) tourism. We never observed an iguana farm meant for meat production operating sustainably as a profitable venture. There seem to be several flaws in the venture for profit from iguana meat production. First, the amount of cash to start up an iguana farm is beyond the scope of most small, local farmers. This is a problem that Magnusson (1984) found at alligator farms in the US with the average owner investing over $3,000,000 in facilities alone. Secondly, due to length of time to maturity and upkeep costs, it is difficult to raise captive iguanas to a harvestable size for meat consumption and still remain profitable (Burghardt and Rand 1982; Fitch et al. 1982; Werner 1987). Finally, due to the high cost of breeding iguanas in captivity, it is unlikely to be profitable while there are still wild animals available (Eilers et al. 2002), a sentiment shared by many farmers. One farmer specifically told us that it was much easier and cheaper to capture an iguana in the wild than to raise an individual to a profitable size for consumption.

Our results point towards the highest probability for farmers to make profits from iguanas is by selling hatchlings into the pet trade. The iguana market is dominated by commercial farms that infrequently purchase any shortages of animals from local farmers. More importantly, demand in the iguana pet market has decreased significantly since the 1990s. In our study, we saw evidence of many local farms catering to the pet trade had stopped raising iguanas and closed due to lack of demand for *I. iguana* hatchlings. Two of the five commercial pet breeding facilities were expected to shut down soon due to various economic and legal exportation problems. Even the largest commercial breeding operation was planning to downsize its iguana output. The declining interest in iguanas as pets and faddish nature of pet reptile trade production makes iguana farming a short-term, unstable venture. Tourism ventures for iguanas were not profitable by themselves and relied on outside funding to persist. While iguana tourism may have some benefits in educating visitors about the species, it does not fulfill the ultimate goal of profitability.

We found that virtually all of the farms we spoke with relied on funds from NGOs, government agencies, or private donations. Only one of the commercial breeding operations operated without government or NGO funds and was completely independent of any aid, and this was a large-scale reptile exporter with *I. iguana* breeding stock of approximately 25,000 animals. A second medium sized pet farm received only veterinary assistance from the local university.

Support was not found for the objective of iguana farms providing affordable meat for local populations. We did not see evidence of any supply chain where animals were brought to market or being sold. The profit margins are simply too small and the investment too great for the cheap production of meat. Iguanas are still eaten widely in Central America, but people predominantly consume wild caught animals (L. Ruyle unpub. data). Eilers et al. (2002) in an earlier review, found only 12% of meat production farms selling iguanas, which were mainly founder animals for other farms. The farmers we interviewed ate iguana meat typically only for medicinal purposes, citing boredom of the taste. *I. iguana* and *C. similis* can be found for sale in markets, but from our investigations it does not seem that these animals were being captured near any of the community farm areas. We found only one case of prepared iguana purchased from farms, although we were unable to determine from which farm she purchased the meat.

We saw no evidence that iguana farming alleviated pressures on wild populations though reduction in hunting or by providing new animals through release programs. Several interviewees stated that it was easier and cheaper to hunt wild iguanids rather than farm them. We also observed several people selling wild caught iguanas on the roads next to farms. Although various NGO protocols outline release of a certain percentage of hatchlings into the wild, we did not find any farms following protocols, rather they sold them to larger farms looking to fill in shortages in their orders for the pet trade. The potential profitability of the pet trade circumvents the intent of releasing hatchlings into the wild as a mitigation strategy. In contrast to augmenting populations it is possible that stock brought from other areas of Central America may bring novel parasites or pathogens to naïve populations of local iguanids creating new threats for conservation of the species (Daszak et al. 2001). Releasing iguanas into the wild after being raised in captivity increases the risk of zoonotic disease transfer from humans or other iguanas. Additionally, bringing in stock animals from other areas may introduce diseases across habitats and countries. Finally, we found one instance where a tourist attraction catering to cruise ship tourists was created for the likely non-native *I. iguana*, on an island that supports an insular endangered endemic species of *C. oedirhina. I. iguana* roams free and is supplementally fed, while native predators like *Boa constrictor* are killed. Large densities of *I. iguana* may pose risk to *C. oedirhina* by promoting diseases (Daszak et al. 2001) or parasites (Wikelski 1999) to an already geographically limited and endangered species. These animals are strictly for viewing and not consumed. Therefore, in this instance, an iguana farm may actually be more detrimental to the conservation of iguanids than having any sort of alleviation on pressures for wild populations.

The majority of the farms we interviewed cite conservation, not profitability, as one of the key reasons for their existence. Magnusson (1984) reported similarly that alligator farms in the US stay viable mainly due to interest in alligators, not profitability. We have doubts as to whether the original concept as implemented or as how it is currently being practiced would serve as an effective conservation measure. We feel that farms may actually reduce the incentive for conservation of wild populations by encouraging consumption of species that are cheaper to hunt than farm. Magnusson (1984) also felt crocodilian farming reduced incentives for conservation by encouraging use of species where captive propagation cannot meet low cost demand.

The concept of raising iguanas as an alternative food source was highly celebrated by many groups as a "win-win solution" for conservation of iguanas and poverty alleviation in Central America (Cohn 1989; Gruson 1989; Vaughan 1990; Werner 1989; Werner 1991). However we believe that the main objectives or economic gains, inexpensive meat sources, and reduction of pressures on wild populations have not been met. The sole profitable venture of iguana pet trade is unsustainable. Even though the pet market for iguanas has declined and there is sufficient evidence that it is unprofitable to raise iguanas for food, the impact of the iguana farming model continues today as NGOs continue to propose iguana farming is as a way of both augmenting wild populations and serving as an alternative source of income for local families. We encountered recently proposed programs both in Nicaragua and Honduras for new iguana farms (PROCREA 2009). We feel it is very important that the model for iguana farming should be analyzed thoroughly before being invested in as either a conservation or alternative livelihood measure.

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CHAPTER 5

CONCLUSION

Effective conservation of endangered wildlife requires a multi-disciplinary understanding of issues. Ecological knowledge of species combined with the effects of human activities on those species should be applied when developing conservation programs. Conservation efforts should be evaluated for their effectiveness in meeting both ecological and social requirements for protection of species and impacts on local human populations. My dissertation sought to contribute to conservation efforts of Central American iguanas by using traditional ecological studies for foundational knowledge of a critically endangered species and evaluating the impact of humans living with that species. Additionally, I evaluated iguana farming as a conservation strategy meant to benefit local human populations as well as protect iguanas.

In Chapter 1, I sampled a critically endangered iguanid, *C. melanosterna,* at four sites over three years to describe the relationship between human activity and variation in parasite load, frequency of broken tails, behavior, and density. Two of the sites were characterized by high levels of human activity including domestic animals and trophic subsidies (food waste, water, and refuges) and two of the sites had low levels of human activity and no domestic animals, although one of these sites provided trophic subsidies. Tick loads were not clearly associated with human density or activity, and were instead positively associated with ctenosaur density. Ctenosaurs had a higher frequency of broken tails in areas of high human density with the presence of domestic animals. Larger ctenosaurs and ctenosaurs in areas of high human density fled in closer proximity and shorter distances when approached by investigators, suggesting boldness increases with age and human density. Ctenosaur density was greatest at the site with high human density (food subsidies) and no domestic animals. Ctenosaur density was lowest where there was both high human density and domestic animals present. My results show that human activities are affecting ctenosaur populations, but the effects are context dependent. My work suggests subsidies in the form of garbage promote bolder behaviors by ctenosaurs, however, the presence of domestic animals results in higher injury rates and ultimately a lower density of lizards.

In Chapter 2, I present data on the life history and demographic patterns of a critically endangered, insular reptile species, *Ctenosaura melanosterna,* based on a long-term capture-mark-recapture study. I estimated body size, growth rates, age, and age structure of the ctenosaur population on Cayo Menor at the research site. In addition, I estimated annual survival and capture probabilities, population size, and population growth rates of this population. Finally I used these data to evaluate population persistence using Monte Carlo simulations in a population viability analysis (PVA) with the goal of evaluating extinction risk and estimating sensitivity to catastrophic events. My paradoxical results suggest that more data or a different PVA approach are needed to better explain the survival probability of the *C. melanosterna* population at Cayo Cochino Menor. My estimates of population size or growth rate may be biased due to the limited temporal scope of the study. Additionally, more data on recruitment, hatchling survival, and accounting for adult population sex differences will help refine PVA estimates on subsequent analyses. I also hope to run different models of PVAs, particularly one that uses only females in the future. Our data were limited to the area immediately around the research station; therefore while we feel these data useful in the short term, we recommend that studies further monitor population growth rates on a larger scale both temporally and spatially to fully ascertain the trajectory of the species.

In Chapter 3, I evaluated iguana farming as a conservation strategy in Central America. Specifically, I sought to understand the outcomes for the primary objectives of providing a) an alternative source of income for people that would otherwise harvest animals from the wild, b) sustainable protein source for local communities or c) alleviation of pressures of consumption for wild populations. I examined these questions by visiting facilities and interviewing people farming iguanids in Central America. I documented the history of iguana farming and reported on the status of farms operating from 20 years to start-ups. Despite the popularity of the concept, I found little evidence that iguana farms are profitable for meat, that any farms sell stock primarily for consumption, or that farms alleviate pressures on iguanids in the wild. I argue that farms may actually work against conservation by encouraging animals to be sold into the pet trade, and possibly putting wild populations in danger from release of farm animals that may carry parasites or disease because they were brought in as stock from other areas or as a consequence of farming practices.

In conclusion, my dissertation contributed to the conservation of *Ctenosaura melanosterna* by investigating impacts of human activities on the lizard and providing the first baseline data set for the species. It also contributed to the greater conservation of iguanas everywhere by rejecting the efficacy of iguana conservation as a mitigation tool. My dissertation blended social and biological sciences to provide a solid foundation to conserve the species.