Long-term trends in the demography of the Allen Cays Rock Iguana (Cyclura cychlura inornata): Human disturbance and density-dependent effects

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ABSTRACT

Allen Cays Rock Iguanas (Cyclura cychlura inornata) are native to two small islets (Leaf and U Cay) in the north-central Bahamas. These populations were nearly extirpated in the early 1900s because of heavy hunting pressure (for food), but increased to a total of ca. 150 lizards in 1970, and now number over 500 (not including juveniles). Over the past several decades poaching has declined, but tourist visitation (including nearly daily supplemental feeding of iguanas) has increased. To examine human impacts on the demography of these iguanas, survival, population growth rates, and population sizes for subadult and adult (>25 cm snout-vent length) males and females on the two cays were estimated based on mark–recapture data collected over a 25-year period (1980–2004). As predicted, annual survival probability was higher on U Cay (with less human visitation) than on Leaf Cay, was higher in females than in males (which are bolder), and exhibited a declining trend. Both populations more than doubled during this study, but population growth rates declined to near zero in recent years. These data reflect the importance of human impacts, but also suggest that the populations may be nearing carrying capacity. The rapid population growth observed on these cays, and that seen for several other translocated iguana populations, suggest that if unnatural causes of mortality are reduced or eliminated, island populations of iguanas are capable of rapid recovery. The inexpensive establishment of assurance colonies on undisturbed “islands” should be considered for any comprehensive management plan for endangered species of iguanas.

1. Introduction

As remote locations become more accessible, and as rates of human visitation to remote locales increase, populations of threatened or endangered animals and plants (as well as some healthy populations) face new threats and challenges. For example, increased interactions with humans, often as a result of increased tourism, have been shown to affect a range...
of vertebrates, including birds (Steidl and Anthony, 2000; McClung et al., 2004; Müller et al., 2004; Blumstein et al., 2005), mammals (Boydstun et al., 2003; Manor and Saltz, 2003), amphibians (Rodríguez-Prieto and Fernández-Juricic, 2005), and reptiles (Garber and Burger, 1995; Labra and Leonard, 1999; Romero and Wikelski, 2002; Kerr et al., 2004). Such disturbance can have negative effects on the long-term viability of populations, either through decreased reproductive success, increased mortality, or reduced access to resources (Garber and Burger, 1995; Steidl and Anthony, 2000; Yorio et al., 2001; McClung et al., 2004; Rodríguez-Prieto and Fernández-Juricic, 2005).

Long-lived lizards, especially those that live on islands, are especially vulnerable to human disturbance (Alberts, 2000; Romero and Wikelski, 2002; Lacy and Martins, 2003; Knapp, 2004; Pregill and Steadman, 2004). However, evaluating the real and potential impacts of increasing human disturbance requires good basic life history data, as well as information about changes to demographic parameters in populations exposed to humans. Unfortunately, although considerable research has been done on the life history of short-lived lizards (Dunham and Miles, 1985; Shine and Charnov, 1992; Niewiarowski et al., 2004), much less work has focused on long-lived lizards (i.e., those that mature at >5 years; e.g., reviews in Huey et al. (1983) and Vitt and Pianka (1994)). This is particularly troublesome because long-lived lizards are disproportionately under threat of extinction, especially those on islands (Alberts, 2000; IUCN, 2000), at least in part due to their particular life histories (delayed maturity, low reproductive rates, sensitivity to adult survival). But because of their long lives, obtaining multi-generational data to quantify life history traits and to permit population modeling with the goal of developing sound management strategies is often time-consuming and expensive. This is further complicated because so many populations of long-lived lizards are in decline and/or are too rare to make field work feasible even over the short term (Alberts, 2000), and thus not likely to provide accurate measures of demographic parameters or their normal variation under natural (i.e., undisturbed) conditions. This places a high premium on the immediate study of the least disturbed long-lived species in order to provide baseline demographic data for managing those species in the future, for identifying factors that may contribute to population increases and declines, and for extrapolation to similar but imperiled species with the goal of reversing their declines.

To date, long-term studies of long-lived lizards under conditions of minimal human disturbance have been confined to the Galápagos Islands (Snell and Tracy, 1985; Laurie and Brown, 1990a,b; Cayot et al., 1994; Wikelski and Thom, 2000; Wikelski and Romero, 2003), the Turks and Caicos Islands (only four years; Iverson, 1979), and the Bahamas (Iverson et al., 2004a,b). The latter site has been studied since 1980 (only a few months shorter than the longest study in the Galápagos; Snell and Tracy, 1985), and has provided the most detailed life history data available for a long-lived lizard species (the Allen Cays Rock Iguana, Cyclura cychlura inornata) outside the Galápagos, including data on growth (Iverson et al., 2004a), and reproductive output and nesting ecology (Iverson et al., 2004b). In addition, Iverson et al. (2004b) reported estimates of survival in the nest, but only preliminary estimates of adult survival have previously been generated (Iverson, 2000).

The Allen Cays Rock iguana, the most northerly member of its genus (24.75° N latitude), is known to occur naturally on only two cays in the Allen Cays of the northern Exuma Islands in the north-central Bahamas: Leaf Cay (4 ha; 4 m maximum elevation) and U Cay (3 ha; 9.5 m). In 1892 C.J. Maynard found Allen Cay iguanas to be “not uncommon” on U Cay, but when he was storm-bound off the island in early March of 1915, he could find only two (Barbour and Noble, 1916). Both of those were shot; one became the holotype and the other escaped. Hence, Barbour and Noble (1916) believed that the Allen Cays iguana was “beyond doubt extinct” (see also Barbour, 1937) because of human removal for food. However, although Maynard apparently had “ample opportunity to cover U Cay” completely (Barbour and Noble, 1916), the weather was inclement during his visit, and most of the population likely remained out of sight, within retreats. Indeed, the density of the vegetation on some parts of the islands, the small size of juveniles, and the abundance of inaccessible cavities in the honeycomb limestone into which the iguanas can retreat make it doubtful that humans could directly remove every iguana from either Leaf or U Cay. Nevertheless, early editions of the “Yachtsman’s Guide to the Bahamas”, published annually since 1956, also reported that iguanas were extinct in the Allen Cays (Carey, 1976).

When Wayne King (personal communication) visited the Allen Cays in August of 1964, he reported that iguanas “while still extant, [were] not thriving”. Six years later, in late March of 1970, Carey (1976) used two (undefined) survey techniques to estimate the population of iguanas on Leaf Cay at 65 and 73. He did not systematically survey U Cay, but speculated that the population there was “at least equivalent to that of Leaf Cay”. Field observations by the authors suggested that the populations have increased substantially since then, perhaps indirectly due to the passage of the Wild Animals Protection Act by the Bahamas government in 1968 (Sandra Buckner, personal communication). That law provided legal protection for the Allen Cays Rock Iguana for the first time, and hunting pressure has apparently declined since then. However, this iguana is still considered Endangered by the IUCN because of its restricted range, its small population size, and its vulnerability to hurricanes (Alberts, 2000). In addition, some poaching still occurs (for consumption and for the illegal pet trade) and tourist visitation has increased since 1970, with nearly daily supplemental feeding today (Fig. 1). Up to 150 visitors/day now visit Leaf Cay (most on powerboat tours that arrive at 1000 h and 1600 h, feed fruits to the iguanas, and leave after 30–45 min), and only up to 25/day visit U Cay (inaccessible to powerboats). Feeding by tourists seems not to have affected average growth rates of individual iguanas over the past two decades (Iverson et al., 2004a). However, while these lizards are almost completely herbivorous by nature (e.g., Alberts, 2000), they readily accept and consume almost any item thrown to them by tourists (from brownies to bread to ground beef to styrofoam; personal observations). The direct impact of this activity on individual lizards is not known, but it is suspected that it might affect their survival.

Because the two inhabited islands have similar areas, have no invasive vertebrate species, supported iguana populations
of similar size in 1970 (Carey, 1976), and the average growth rate of individual iguanas between 1980 and 2000 was similar (Iverson et al., 2004a), these islands are an ideal system in which to examine the effects of tourist visitation, as well as the reduction in poaching, on iguanas. This paper analyzes 25 years of mark–recapture data from Allen Cays rock iguanas to estimate survival rates, as well as population sizes and population growth rates.

The authors predicted that because males appear to be more bold than females (JBI, GRS, JMV; personal observations), they should be more strongly impacted by humans (via misfeeding, poaching, or simple mischief). Hence, survival in males should be lower than in females. It was also predicted that because Leaf Cay is visited by humans significantly more than U Cay, survival rates should be higher on U Cay than on Leaf Cay. Since tourist visitation has increased over the last 25 years, the data were also examined for evidence that these effects might have increased over that time. Finally, because of the reduction in poaching during the last 25 years, and the apparent increases in population sizes during that time, the possibility that these populations are nearing carrying capacity is discussed.

2. Materials and methods

2.1. Field methods

Populations of Allen Cays rock iguanas (C. c. inornata) were sampled on Leaf Cay and U Cay in the Allen Cays, northern Exuma Islands, Bahamas in 17 of 25 years from 1980 to 2004. A detailed study area description is provided by Iverson et al. (2004b). These are believed to be the only natural populations of this subspecies, because their presence there has been known from at least 1892 (Barbour and Noble, 1916). Introduced populations are known from at least four other cays in the northern Exumas (Knapp, 2001; Iverson, unpublished). Sampling effort on Leaf and U Cays was variable, with a general increase over time. In 1980, one researcher (JBI) spent only a few hours in mid-March on each island. From 1982 through 2000, at least 6–12 researchers spent five days in mid-March capturing and marking as many iguanas as possible. During mid-May in 2001 through 2004, at least 13 researchers spent 5–6 days capturing and processing iguanas. From mid-June to mid-July in 2001 and 2002, three researchers also captured and marked iguanas while studying the nesting ecology of females (Iverson et al., 2004b).

Captured iguanas were uniquely marked by toe clips (three toes maximum) following Ferner (1979), since toes are sometimes lost naturally in this genus (Carter and Hayes, 2004; Iverson, unpublished), and toe-clipping has been shown to have little effect on cursorial lizards (Dodd, 1993; Borges-Landáez and Shine, 2003; Langkilde and Shine, 2006). Between 1993 and 2004, 572 iguanas were also injected with PIT tags (Info-Pet™; passive integrated transponder). Iguanas were sexed by cloacal probing (Dellinger and von Hegel, 1990) and released as soon after capture as possible (usually within a few hours; always within 24 h). Full details of capture and processing methods were presented by Iverson et al. (2004b).

Juvenile Allen Cays iguanas (particularly young of the year) are difficult to capture as reliably as subadults and adults. However, by about 6.5 years of age, and about 20 cm snout-vent length (SVL), they are easily detected and can then usually be captured when located (personal observations). Because of this, analyses were limited to captures of subadult and adult iguanas >25 cm SVL (nearly all >8.5 years of age Iverson et al., 2004a).

2.2. Demographic analyses

A three-step analytic process was used for the demographic analyses, which consisted of: (1) modeling capture probability ($p$), (2) modeling survival probability ($\phi$), and (3) modeling population growth rate ($\lambda$). The Cormack-Jolly-Seber model (Cormack, 1964; Jolly, 1965; Seber, 1965), generalized by Lebr-
et al. (1992), was used to estimate, from a joint likelihood function, capture probability (p) and apparent survival (\( \phi \)). Apparent survival is the probability of surviving and remaining on the study area, which is here equivalent to true survival because natural, successful emigration from the islands is essentially impossible. Pradel's (1996) reverse-time model was used to estimate population growth rate (\( \lambda \)). The Pradel model is an extension of the Cormack–Jolly–Seber model, where \( \lambda \) may also be estimated in a joint likelihood function with capture (p) and apparent survival probabilities (\( \phi \)). Analyses were conducted in Program MARK (Version 3.2; White and Burnham, 1999). Although sampling occurred on a less-than-annual basis, annual survival rates and population growth rates were computed by scaling rates computed over longer periods by taking the appropriate root of the rate.

Prior to the analyses, goodness-of-fit (GOF) of the Cormack–Jolly–Seber model was examined using Program RELEASE (Test 2 + Test 3; Burnham et al., 1987), which resulted in \( \chi^2 = 377.4 \) (df = 184), indicating that overdispersion existed in the data, most likely due to heterogeneity in capture and/or survival probabilities among individuals. Therefore, an information-theoretic model selection and multi-model inference approach was used based on AIC (Akaike’s Information Criterion; Akaike (1973)) corrected for both small sample size and overdispersion (QAICc; Hurvich and Tsai, 1989; Lebreton et al., 1992). To account for overdispersion further, variance estimation was adjusted by \( \hat{c} = 2.05 \) (Lebreton et al., 1992; Burnham and Anderson, 2002).

After goodness-of-fit testing, the top-ranked model structure (i.e., the model with the lowest QAICc value and hence, the most supported structure) on capture probabilities was determined by analyzing 10 possible capture probability structures with the fully parameterized \( \phi \) model, \( \phi_{(sex \times cay \times t)} \). This notation follows Lebreton et al. (1992), and indicates full time dependence in survival probabilities, with interactions between sex, cay, and year. The 10 capture probability structures were \( p_{(sex \times cay \times t)} \), \( p_{(sex \times cay + t)} \), \( p_{(sex \times t + cay)} \), \( p_{(sex + cay \times t)} \), \( p_{(sex + cay + t)} \), \( p_{(sex + t)} \), \( p_{(sex + t + cay)} \), \( p_{(cay + t)} \), \( p_{(cay + t)} \), and \( p_{(t)} \), where the symbol “+” indicates main effects only (i.e., no interactions). Thus, for example, the model \( p_{(sex \times cay + t)} \) includes the main effects of sex, cay and time, and the interactions between sex and cay. Only time-dependent structures on capture probability were considered, so as to retain the existing time structure in the data and thus avoid biasing the estimation of time trends in the data (described below).

The mark–recapture data were next submitted to the Cormack–Jolly–Seber model survival analysis, where survival was modeled using the AICc-based top-ranked parameterization of capture probabilities, and parameterizations of \( \phi \) that included three variables: sex, cay, and time trend (T). All combinations of these effects with and without interactions were considered, for a total of 15 models.

Based on this suite of models survival rates and capture probabilities were computed using multi-model inference procedures described by Burnham and Anderson (2002); i.e., model-averaged estimates of survival and capture probabilities were calculated by averaging estimates for all of the models, weighted by Akaike weights (i.e., based on relative AICc values), and unconditional standard errors were calculated as described by Burnham and Anderson (2002).

To estimate population growth rate, the top-ranked model structure from the survival analysis on \( p \) and \( \phi \) was used, and then the same set of structures on \( \lambda \) within the Pradel model was considered for \( \phi \) in the Cormack–Jolly–Seber model analysis; that is, all 15 combinations of sex, cay, and T, with and without interactions. Estimates of population growth rate were computed by model-averaging estimates from this set of models (Burnham and Anderson, 2002), as described above.

Finally, estimates of abundance for each group in the analysis (i.e., two sexes and two cays) and associated standard errors were calculated based on the Williams et al. (2001) estimator of abundance, where abundance in year \( i \) is calculated as

\[ N_i = \frac{n_i}{p_i} \]

with approximate standard error, calculated using a delta-method approximation (Seber, 2002), equal to

\[ SE(N_i) \approx \left( \text{var}(\hat{p}_i) \left(\frac{n_i}{p_i^2}\right) + \left(\frac{n_i(1 - \hat{p}_i)}{p_i^2}\right) \right)^{1/2} \]

where \( n_i \) is the number of individuals captured in year \( i \), and \( \hat{p}_i \) is the estimated capture probability in year \( i \), computed based on model-averaged capture probability estimates from the analysis of survival rates.

3. Results

3.1. Capture probabilities

Through 2004, 1074 individual iguanas had been marked on Leaf Cay (with 2162 additional recaptures; 52.9% of those of determinable sex being male) and 482 on U Cay (plus 1325 recaptures; 57.1% male). The analysis of capture probabilities indicated that the \( p_{(sex \times cay + t)} \) structure was the best model of capture probability, with 75% of the Akaike weight (\( \omega \); Burnham and Anderson, 2002). This structure was used in the subsequent Cormack–Jolly–Seber model of survival probability. Capture probabilities from the survival analysis were variable over years, cays, and sexes, possibly due to variation in the size and skill of the field crews as well as conditions on the islands and variation in individual lizard behavior. The lowest estimated capture probability was 0.23 (SE = 0.10) for females at U Cay in 1982, whereas the highest estimated capture probability was 0.84 (0.03) for males at U Cay in 2001 (Table 1).

3.2. Survival probabilities

The two best model structures for survival probability were \( \lambda_{(sex + cay)} \) with 18.7% of the Akaike weight, and \( \lambda_{(sex)} \) with 18.2% of the Akaike weight, indicating strong sex and cay effects on survival (Table 2). In addition, the presence of a time trend (T) in the structure of the next five best models, with Akaike weights from 12.8% to 7.2%, suggests an apparent, though weak, time trend in survival.

As predicted, estimated survival was lower for males than for females (logit-scale effect estimate from the top-ranked model in which the effect appeared = −0.45; 95% CI = −0.72
The best model structure for population growth rate (\( \lambda \)) in the Pradel analysis was sex + cay + T (36% of the Akaike weight; Table 4). In addition, all of the top four structures (Akaiae weights 16–36%, combined weight, 97%) included sex, cay, and time trend effects, either with or without interactions. Estimates of \( \lambda \) were consistently lower on U Cay than on Leaf Cay, lower in males than females, and decreased over time, from estimates over 1.1 early in the study to estimates near or below 1.0 late in the study (Table 5 and Fig. 2). Despite considerable variation in the population estimates early in the study, estimates of abundance (Table 1 and Fig. 3) indicated that subadult/adult males and (particularly) females of both populations increased over the course of the study, and that the population on Leaf Cay increased faster than on U Cay.

4. Discussion

4.1 Capture probabilities

Estimated capture probabilities supported the impression that males are more bold than females; i.e., they had a greater
tendency to approach humans. However, it can only be speculated as to why males on the less-visited U Cay would be easier to capture compared to those on Leaf Cay. It is possible that the intensity of human interactions on Leaf Cay has actually made some males more skittish there (Ron et al., 1998; Kerr et al., 2004; but see Labra and Leonard, 1999 for the opposite effect). In addition, because there is less feeding of iguanas on U Cay, greater competition among males on that island for the more limited supplemental food may make males more aggressive, and hence, more easily captured. In addition, the behavioral difference may be related to the geographic differences between the islands. Most of Leaf Cay is low and sandy, and habitats there have predominately open substrates (even in the forest understory). Apart from its central open, sandy isthmus, U Cay is mostly rugged limestone (>90%) with nearly impenetrable vegetation. The physiognomy of Leaf Cay is therefore more conducive to thorough sampling than U Cay. It may be that the bolder males on U Cay present themselves on the open, sandy isthmus, whereas the more shy females are able to seek refuge easily in microhabitats more difficult to sample.

4.2. Survival probabilities

There was strong support for the predicted differences in survival between the two cays, with higher rates on U Cay than Leaf Cay, presumably because Leaf Cay experienced much higher tourist visitation. Thus, these analyses support the
Table 5 – Estimates of annual population growth rate ($\lambda$) for male and female iguanas on Leaf Cay and U Cay

<table>
<thead>
<tr>
<th>Interval</th>
<th>Leaf Cay</th>
<th></th>
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<th>U Cay</th>
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<tbody>
<tr>
<td></td>
<td>Males</td>
<td>Females</td>
<td>Males</td>
<td>Females</td>
<td>Males</td>
<td>Females</td>
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<td></td>
<td>$\lambda$ (SE)</td>
<td>$\lambda$ (SE)</td>
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<td>$\lambda$ (SE)</td>
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<td>$\lambda$ (SE)</td>
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<tr>
<td>1980–1982</td>
<td>1.175 (0.024)</td>
<td>1.233 (0.029)</td>
<td>1.124 (0.022)</td>
<td>1.183 (0.026)</td>
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<tr>
<td>1982–1983</td>
<td>1.162 (0.022)</td>
<td>1.218 (0.026)</td>
<td>1.110 (0.020)</td>
<td>1.168 (0.024)</td>
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<td>1983–1986</td>
<td>1.148 (0.019)</td>
<td>1.204 (0.024)</td>
<td>1.096 (0.018)</td>
<td>1.152 (0.021)</td>
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<tr>
<td>1986–1988</td>
<td>1.135 (0.017)</td>
<td>1.189 (0.021)</td>
<td>1.082 (0.016)</td>
<td>1.137 (0.019)</td>
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<td>1988–1990</td>
<td>1.121 (0.015)</td>
<td>1.175 (0.019)</td>
<td>1.068 (0.014)</td>
<td>1.122 (0.017)</td>
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<td>1990–1992</td>
<td>1.108 (0.013)</td>
<td>1.161 (0.017)</td>
<td>1.054 (0.013)</td>
<td>1.108 (0.015)</td>
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<td>1992–1993</td>
<td>1.095 (0.012)</td>
<td>1.147 (0.015)</td>
<td>1.041 (0.011)</td>
<td>1.093 (0.014)</td>
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<td>1993–1994</td>
<td>1.083 (0.010)</td>
<td>1.133 (0.013)</td>
<td>1.027 (0.010)</td>
<td>1.079 (0.012)</td>
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<td>1994–1995</td>
<td>1.070 (0.010)</td>
<td>1.119 (0.012)</td>
<td>1.014 (0.010)</td>
<td>1.065 (0.012)</td>
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<td>1995–1996</td>
<td>1.058 (0.009)</td>
<td>1.106 (0.011)</td>
<td>1.001 (0.010)</td>
<td>1.051 (0.011)</td>
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<td>1996–1998</td>
<td>1.045 (0.010)</td>
<td>1.092 (0.011)</td>
<td>0.989 (0.010)</td>
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<td>1998–2000</td>
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<td>2000–2001</td>
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<td>2001–2002</td>
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<td>0.951 (0.013)</td>
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<td>2002–2003</td>
<td>0.997 (0.014)</td>
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<td>2003–2004</td>
<td>0.986 (0.016)</td>
<td>1.028 (0.017)</td>
<td>0.927 (0.016)</td>
<td>0.971 (0.016)</td>
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Fig. 2 – Annual population growth rate estimates (lambda) and 95% confidence intervals for male (closed circles) and female (open circles) Allen Cays Iguanas on Leaf and U Cays over the last 25 years.

Fig. 3 – Population size estimates (means ± SE) for male (open circles) and female (closed circles) Allen Cays Iguanas on Leaf and U Cays for individuals >25 cm snout-vent length over the last 25 years.
hypothesis of a negative impact of tourists on survival in these iguanas, but do not permit the identification of the precise mechanism for that increased mortality (e.g., via improper feeding, introduction of pathogens, poaching, or direct killing). The survival analysis also indicated a weak, but noticeable decline in survival over the study period, particularly over the last five intervals (Table 3). Part of this decline could be explained by the continuing increase in visitation, but it is more likely related to density-dependent feedbacks in the populations as they reach carrying capacity (see discussion below).

The annual survival estimates of approximately 87–93% for Cyclura cychlura are similar to those for other long-lived lizards. For example, Laurie and Brown (in Table 2, 1990a) reported estimates for Galapagos marine iguanas (Amblyrhynchus cristatus) of 83% for females and 79% for males (91% and 88%, respectively, when an El Niño year was excluded). In addition, Iverson (1979) estimated annual survival at 90% (females) and 95% (males) for Cyclura carinata in the Turks and Caicos Islands. Finally, desert iguanas (Dipsosaurus dorsalis) and chuckwallas (Sauromalus obesus) in southeastern California had estimated annual survival rates of 61% (Krekorian, 1984) and 72–74% (Abts, 1987), respectively.

The finding that mortality in males is higher than in females was corroborated for the Galapagos marine iguana by Laurie and Brown (1990a,b). However, males are larger than females in both these species, and Laurie and Brown (1990b) found that mortality was size-related, such that after controlling for body size, females actually had lower survival probabilities. The higher mortality in males observed in this study may be related to their boldness and hence their greater exposure to predation (e.g., by osprey, herons, or owls; Iverson, 1979; Hayes et al., 2004), harassment by tourists, and/or poaching (Smith and Iverson, 2006). An alternative explanation for this pattern might be the result of vigorous aggressive encounters between males during the breeding season in May. However, females aggressively defend their nest sites against all conspecifics, and for a longer period than the mating season (Iverson et al., 2004b), so the basis for the sexual differences in mortality deserves further investigation.

Preliminary data on survival in adult Caicos Island rock iguanas (Iverson, 1979) suggested that females experienced higher mortality rates than males; however, those data were collected on islands onto which non-native predators had recently been introduced (Iverson, 1979), and which nearly extirpated the population in about 4 years (Iverson, 1978). Those results may reflect the increased vulnerability of nest-guarding female rock iguanas to predation (e.g., see Hayes et al., 2004) by cats and dogs.

4.3 Population growth rate and size

Population growth rates were highest for Leaf Cay females, followed by Leaf Cay males, U Cay females, and U Cay males. The higher population growth rates on Leaf Cay may be attributable to the higher levels of supplemental feeding there (Iverson et al., 2004a,b). However, this result at first seems inconsistent with the higher survival rates on U Cay, and the fact that measures of reproductive output (e.g., clutch size, egg size, and frequency) apparently do not differ between the cays (Iverson et al., 2004b). Furthermore, although primary productivity is certainly higher on Leaf than U Cay (compare color aerial photographs in Iverson et al. (2004b)), and rates of food supplementation on Leaf Cay are also higher, individual growth rates have not been higher on Leaf Cay than U Cay (Iverson et al., 2004a). The slower rate of population growth on U Cay is therefore likely due to lower rates of survivorship in juveniles on that cay. Although sufficient recapture data of juveniles on U Cay to test this assumption are lacking, it is known that nest mortality on U Cay is higher than on Leaf Cay in some years, primarily because the nesting areas are all low and dangerously moist (Iverson et al., 2004b).

Based on estimates of abundance, the population on Leaf Cay has increased from about 100 subadults and adults (>25 cm SVL; see Section 2) in 1982 to perhaps 360 in 2002 (Table 1 and Fig. 3). Indeed, 290 and 286 subadults and adults (453 and 487 total individuals) were captured in 2001 and 2002, respectively. In 2002, based on the proportion of iguanas still lacking paint marks at the end of the field season, the senior author subjectively estimated the entire Leaf Cay population (including juveniles) at about 600, excluding young of the year. The total mass of 484 of the iguanas actually captured on Leaf Cay in 2002 was 376.3 kg (a minimum standing crop biomass of 94.1 kg/ha), which is among the highest values yet recorded for an iguana (Table 6) or any other lizard (Iverson, 1982; Rodda and Dean-Bradley, 2002).

Similarly, the population on U Cay is estimated to have increased from about 127 subadults and adults in 1982 to about 167 in 2002. For comparison, 136 and 127 subadult and adult iguanas (166 and 179 total) were actually captured on U Cay in 2001 and 2002, respectively, and the total population in 2002 was subjectively estimated at about 300, excluding young of the year. The total mass of 169 of the iguanas captured on U Cay in 2002 was 212.9 kg (a minimum of 71.0 kg/ha).

It is important to note that estimates of abundance as computed here are sensitive to the assumption of equal capture probability over individuals (Williams et al., 2001). However, the entire island was searched during each survey in order to minimize this bias. In addition, there was no trend toward lower estimates of capture probability early in the study. Finally, the estimates of population sizes on the two cays are reasonable given the estimates in 1970 (Carey, 1976), and the actual captures in 2001 and 2002.

These data suggest that the combined Leaf and U Cay subadult and adult populations have increased from only a few individuals during the first half of the 1900s to perhaps 150 in 1970, to about 230 in 1982, and to about 529 in 2002, a rate of increase of about 4% per annum since 1970. Although this is a reassuring recovery rate given the plight of West Indian iguanas, it is far less than the maximum potential for this taxon. Indeed, a population of eight subadult Allen Cays iguanas introduced to Alligator Cay in the central Exuma Islands (6 in 1988; 2 in 1990) grew to about 75 and 90 individuals by 1998 (Knapp, 2001), an annual increase of at least 32% (8–75 in 8 years).

Allen Cays rock iguanas are apparently not the only iguanas with such a great potential for population growth. A few Cuban iguanas (Cyclura nubila) escaped in the mid-1960s to Isla Magueyes off Puerto Rico (Rivero, 1978), and increased to perhaps 157 adults and 10 juveniles in the mid-1980s (Christian, 1986). If it is conjectured that 6–12 individuals
originally escaped, annual estimates of increase would have been at least 14–18% over those 20 years. In addition, five Acklins Bight iguanas (*Cyclura rileyi nuchalis*) were introduced to Bush Hill Cay in the (current) Exumas Cays Land and Sea Park in 1973 (Sandra Buckner, unpublished). In 1997 Haynes et al. (2004) captured 53 individuals on Bush Hill and estimated that the population had grown to about 300 individuals (a rate of increase of 19% per year). Based on 250 captures (58 recaptures) between 2002 and 2004, simple Lincoln-Peterson Index estimates for the island were 315–325 (excluding juveniles) in May 2004 (Iverson, unpublished). If the total population was conservatively estimated to be 350 in 2004, an annual rate of increase of at least 19.9% per year.

These recovery rates instill optimism in the potential to bring West Indian iguanas back from the brink of extinction, provided that direct and indirect human effects on iguana mortality are eliminated (or at least reduce significantly). While the populations on these two cays have increased substantially over the course of the study, there is also evidence of the impact of human disturbance. Of course, reducing human effects on mortality is more easily said than done (Burton, 2004; Wilson et al., 2004; Bradley and Gerber, 2005). However, this study suggests that establishing assurance colonies of endangered iguanas on small islands near to natural (presumably disturbed) populations may be extremely cost-effective and would likely have a high probability of success (Lazell, 2000; Towns and Ferreira, 2001; Knapp and Hudson, 2004) if they are sheltered from human disturbance. In addition, this strategy would dilute the impact of a devastating hurricane. Hence, despite the arguments of some workers against translocations (Dodd and Seigel, 1991; but see debate in Burke (1991); and Reinert (1991), and the closing paragraph of Dodd and Seigel (1991)), relocations should at least be considered during the development of any recovery plan for an endangered iguana.

In many respects the West Indian iguanas of the genus *Cyclura* would seem to be a classic example of a density-regulated species (Roff, 2002), with the most delayed maturity of any known lizard, the production of relatively few large eggs, and parental care in the form of nest guarding (Iverson et al., 2004b). However, the species is also capable of extremely rapid population growth in island environments with low competition and predation. Hence, its colonization (or recolonization) ability mirrors that of species experiencing much more density-independent selection. The ability of these lizards to exhibit such exponential population growth is likely adaptive for these large lizards in island environments influenced by stochastic events like hurricanes in the short term, and sea level changes in the longer term.

The high values for standing crop biomass and the decline in lambda over the last 25 years suggest that the Allen Cays iguana populations may be near carrying capacity ($K$). This possibility begs the questions as to what $K$ is for Allen Cays iguanas on Leaf and U Cays, and how population growth will be mediated as it is reached. Whether density-dependent effects will be greatest on growth, reproduction, or survival remains to be determined (see Massot et al., 1992).

Comparisons of current life history parameters in the Allen Cays (Iverson et al., 2004a,b; this study) with those from the recently introduced population on Alligator Cay (Knapp, 2000, 2001), as well as those from future study in the Allen Cays should address these questions. The effects of the high levels of food supplementation on Leaf Cay during this period should also be illuminating.

Acknowledgements

This paper is dedicated to Mrs. Sandra Buckner, Past President of the Bahamas National Trust, who has supported our work with iguanas in nearly every imaginable way, from providing logistical and historical information, obscure literature, aerial and ground photographs, gear storage, transportation, accommodations, field assistance, and pleasurable company in the field and in Nassau for so many years. She has unselfishly supported nearly every herpetological matter in the

### Table 6 – Standing crop biomass (kg/ha) of populations of West Indian iguanas (genus Cyclura)

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Location</th>
<th>Age class</th>
<th>Biomass</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. c. carinata</td>
<td>Caicos Islands</td>
<td>Adult</td>
<td>17.0</td>
<td>Iverson (1979)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Juvenile</td>
<td>5.2</td>
<td>Iverson (1979)</td>
</tr>
<tr>
<td>C. c. cyclura</td>
<td>Leaf Cay</td>
<td>All</td>
<td>~26</td>
<td>Carey (1976)</td>
</tr>
<tr>
<td>inornata</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>U Cay</td>
<td>All</td>
<td>94.1</td>
<td>Iverson, unpublished</td>
</tr>
<tr>
<td></td>
<td>Alligator Caya</td>
<td>All</td>
<td>71.0</td>
<td>Iverson, unpublished</td>
</tr>
<tr>
<td>C. c. ffiginsi</td>
<td>Guana Cay</td>
<td>All</td>
<td>~26</td>
<td>Carey (1976)</td>
</tr>
<tr>
<td></td>
<td>Anegada</td>
<td>Adult</td>
<td>11.6</td>
<td>Carey (1976)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Juvenile</td>
<td>21.1</td>
<td>Carey (1976)</td>
</tr>
<tr>
<td>C. r. rileyi</td>
<td>San Salvador</td>
<td>All</td>
<td>3.1–22.5</td>
<td>Hayes et al. (2004)</td>
</tr>
<tr>
<td>rileyi</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>White Cay</td>
<td>All</td>
<td>3.7</td>
<td>Hayes et al. (2004)</td>
</tr>
<tr>
<td>c. cristata</td>
<td>Alligator Cay</td>
<td>All</td>
<td>23.7–58.9</td>
<td>Hayes et al. (2004)</td>
</tr>
<tr>
<td>r. nuclalis</td>
<td>Acklin Bight</td>
<td>All</td>
<td>104.4</td>
<td>Hayes et al. (2004)</td>
</tr>
<tr>
<td></td>
<td>Bush Hill Caya</td>
<td>All</td>
<td>~109</td>
<td>Iverson et al., unpublished</td>
</tr>
<tr>
<td></td>
<td>Bush Hill Caya</td>
<td>All</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

a Introduced populations.

b Minimum estimate based on density (47/ha) and mean body mass of non-founders (1.288 kg).
Bahamas for over 14 years, and has facilitated the pursuit of knowledge and conservation of reptiles and amphibians in that country more than any other person.

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REFERENCES


