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# EFFECTS OF TOURISM ON BODY SIZE, GROWTH, CONDITION, AND DEMOGRAPHY IN THE ALLEN CAYS IGUANA, *CYCLURA CYCHLURA INORNATA*, ON LEAF CAY, THE BAHAMAS

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**Abstract.**—The feeding of wildlife by ecotourists has become increasingly popular, but its effects are not well studied. The endangered Allen Cays Iguana is known to occur naturally on only two small cays in the northern Exuma Islands (The Bahamas). One of those cays, Leaf Cay (4 ha) has an easily accessible beach to which up to 150 people converge each day to feed the iguanas. However, iguanas from other parts of the cay rarely ever see an ecotourist. This study investigated the differences in body size, growth, body condition, and demography of the iguanas on opposite sides of Leaf Cay. Iguanas on the human-impacted side of the cay were larger, grew faster, and weighed more (relative to body length), but had similar survival rates as those without human interaction. Capture sex ratios did not differ between sides of the cay and were generally not different from a 1:1 ratio. Although these data might be interpreted as positive impacts of supplemental feeding, when viewed with previously published differences in behavior and blood chemistry, the long-term effects of these feeding activities are of potential concern.

**Key Words.**—ecotourism; feeding; Rock Iguana; The Bahamas

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## INTRODUCTION

The impacts of ecotourism on ecosystems are relatively under-studied compared to recent increases in such activities. For example, increased recreational use of nature preserves or other natural areas can have diverse direct and indirect negative impacts on local ecosystems (Boyle and Samson 1985; Garber and Burger 1995; Rodríguez-Prieto and Fernandez-Juricic 2005; Kangas et al. 2010; Wells et al. 2012). Iguanas are one group that might be impacted, both positively and negatively, by ecotourism (Knapp 2004).

One common activity associated with some so-called ecotourism is the feeding of wildlife (Orams 2002). Natural trophic subsidies can have myriad effects on food webs (see review in Polis et al. 1997). Human supplementation or subsidization of food in a variety of contexts has been shown to increase reproduction but decrease adult survivorship in birds (Arcese and Smith 1988; see review of effects on bird populations in Robb et al. 2008), increase body and liver condition in fish (Dempster et al. 2011), increase the abundance of coyotes (Rose and Polis 1998; Fedriani et al. 2001), and increase body mass in Grey Foxes (Harrison 1997). Thus it is no surprise that anthropogenic supplementation of food associated with ecotourism may be expected to have impacts on the species being fed, as well as other species in the community.

Among lizards, approved feeding of Komodo Dragons (*Varanus komodoensis*) by tourists induced a numerical

response by the lizards, and increased their density at feeding sites while feeding was conducted (Walpole 2001). In another large lizard, the use of human food waste by *Varanus varius* resulted in larger lizards and more male-biased sex ratios at such subsidized sites, at least in the short-term (Jessop et al. 2012). In both of these cases, the studies did not last long enough to evaluate potential longer-term effects of the supplementation.

The Allen Cays Rock Iguana (*Cyclura cychlura inornata*) is endemic to two islands in The Bahamas (Leaf Cay and U Cay) (Fig. 1), and is listed as Endangered by the IUCN Red List of Threatened Species. These two cays are a popular destination for tourists, yachtspeople, and locals, because the iguanas associated with the main beaches have become acclimated to supplemental feeding. Whereas this feeding was only occasional back in the 1980s (Iverson et al. 2006), it is now done daily, and by large numbers of people. The main beach on Leaf Cay has particularly extensive contact with humans, with the daily arrival of 3–5 powerboats carrying as many as 150 people each day to feed the iguanas (Fig. 2; Iverson et al. 2006). This feeding activity has resulted in an unnatural concentration of iguanas on the feeding beach. For example, in 2008 when we sampled 289 iguanas on Leaf Cay (ca. 50% of the subadult and adult population on the cay), 68% of the captured iguanas were present on or immediately adjacent to the feeding beach which comprises only 2% of the total island area.

However, based on our mark-recapture censuses, iguanas on the opposite side of Leaf Cay (4 ha total area) apparently never visit the feeding beach. Hence, this situation allows a direct comparison to be made of fed versus unfed iguanas in the same genetically homogeneous population (Aplasca 2013). We investigated this system in order to examine the impact of tourist feeding on the body size, growth, condition, and demography of the iguanas. The long-term nature of our study allowed for in-depth analysis of these parameters relative to the development of the tourism industry (Iverson et al. 2004b). Specifically, we compared data from Leaf Cay over a 14-year period for subadult and

adult iguanas on the feeding beach versus iguanas from other parts of the island away from the beach to determine the possible effects of supplemental feeding by humans.

#### MATERIALS AND METHODS

This study began in 2000 and involved nearly annual sampling through 2013 (see full study site description and general methods in Iverson et al. 2004b). Sample dates included: 19–21 and 23 May 2000; 9–10 and 13–14 May, and 15 June–11 July 2001; 15–17 and 20 May, and 15 June–13 July 2002; 14–15, 17, and 19 May 2003; 11–13 and 16 May 2004; 13–16 May 2005; 11–13 and 16 May 2008; 17–19 May 2009; 12–14 May 2010; 16–17 and 19 May 2011; and 16–18 and 21 May 2013. Data within each year were considered a separate sample. Iguanas were captured by a team of up to 15 workers using dip nets, nooses, baited live traps, or by hand. Individuals were identified by unique toe clip combinations and PIT tags. Snout-vent length (SVL) and tail length (TL) were measured to the nearest mm, and body mass (BM) was measured to the nearest 5 g. Juveniles < 20 cm SVL were aged by their size cohort following Iverson et al. (2004a), and subsequently aged by the time interval until their recapture. Iguanas were released immediately after processing in the general area where they were captured.

For this study we only included data from iguanas that had been repeatedly (and only) captured on the feeding beach (i.e., fed, with high human interaction) or on other parts of the cay (non-fed, with minimal human interaction). Data from males and females were analyzed separately. Means are given  $\pm 1$  standard error (SE).

We calculated the mean SVL of the 10 largest males and the 10 largest females captured from each side of the island during each survey visit (if fewer than 10 individuals were captured for any category of iguanas in any year, we used all individuals captured). We used an ANCOVA on these mean SVLs with site as a factor and year as the covariate for each sex separately.

To test for differences in growth between fed and non-fed sites, we employed two approaches. The first test employed ANCOVA (SVL) or ANOVA (BM) of growth rate (GR; [final SVL or BM – initial SVL or BM]/interval between initial and final capture;  $\text{cm yr}^{-1}$  or  $\text{g yr}^{-1}$ ) with site and sex as factors and mean SVL for the interval between first and last capture as covariate for SVL growth rate (mean SVL was not a significant covariate for BM growth rate). The second approach used regression of log-transformed data from actual age versus SVL for all captures. We used ANCOVA to compare these regressions by site, separately by sex.

We used two approaches to compare body condition (i.e., body mass relative to body length) of iguanas from the feeding beach versus residents from the opposite side of the cay. First, residuals from the SVL–BM regression

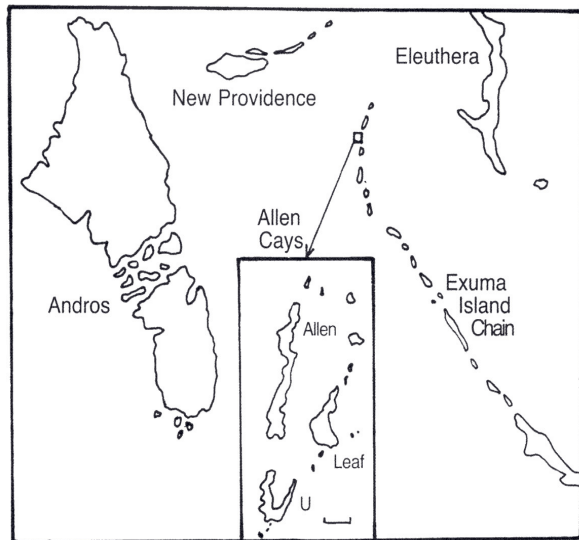


FIGURE 1. Map of study island for Allen Cays Iguanas in the Exumas Islands, The Bahamas. Scale in inset is 200 m.



FIGURE 2. Tourists feeding Allen Cays Iguanas on the main beach on Leaf Cay, The Bahamas. (Photographed by Hannah Lugg).

(log transformed) for the last capture for each individual (Jakob et al. 1996; Schulte-Hostedde et al. 2005) was analyzed for each sex separately (male equation:  $\log\text{BM} = -1.37 + 2.97 \log\text{SVL}$ ,  $n = 161$ ,  $r^2 = 0.74$ ,  $P < 0.0001$ ; female equation:  $\log\text{BM} = -1.44 + 2.99 \log\text{SVL}$ ,  $n = 152$ ,  $r^2 = 0.79$ ,  $P < 0.0001$ ). Second, we compared body condition using Fulton's K (Cone 1989; Stevenson and Woods 2006). Considerable controversy surrounds the use of the first of these (García-Berthou 2001; Green 2001; but see Schulte-Hostedde et al. 2005), but it does produce values with dimensions that are biologically interpretable; whereas Fulton's K is dimensionless (Cone 1989). Using both approaches (assuming corroborated results) would provide increased confidence in our interpretations.

We calculated sex ratios for each year's sample using only subadults and adults  $\geq 20$  cm SVL. We also submitted our capture/recapture matrix (only for subadult or adult iguanas  $\geq 20$  cm SVL) to Program MARK to obtain annualized survival estimates and capture probabilities using the Cormack-Jolly-Seber method (White and Burnham 1999), separately for males and females. In all cases, the model including annual variation in both survival estimates and capture probabilities was the best model or the second best model with AICc values very close to the best model. We thus present the results of the models including variation in both survival estimates and capture probabilities. We used paired  $t$ -tests to compare survival estimates and capture probabilities between the feeding beach and the rest of the cay for males and females separately.

## RESULTS

**Body size.**—The mean SVL of the largest males was greater for the feeding beach than the rest of Leaf Cay (Fig. 3A; Site effect:  $F_{1,19} = 96.4$ ,  $P < 0.0001$ ). For both sites, the mean SVL of the largest males captured each year declined over the course of the study (Fig. 3A; Year effect:  $F_{1,19} = 6.4$ ,  $P = 0.021$ ; Mean  $\text{SVL}_{\text{feeding beach}} = 51.3 - 0.12[\text{Year}]$ ; Mean  $\text{SVL}_{\text{Rest of Leaf Cay}} = 59.8 - 0.26[\text{Year}]$ ). The interaction term between site and year was not significant, indicating that the slopes were not significantly different.

The mean SVL of the largest females was significantly greater at the feeding beach than for the rest of Leaf Cay (Fig. 3B; Site effect:  $F_{1,19} = 200.6$ ,  $P < 0.0001$ ). As with males, mean SVL of the largest females captured each year decreased significantly over the course of our study (Fig. 3B; Year effect:  $F_{1,19} = 5.1$ ,  $P = 0.036$ ; Mean  $\text{SVL}_{\text{feeding beach}} = 37.8 - 0.042[\text{Year}]$ ; Mean  $\text{SVL}_{\text{Rest of Leaf Cay}} = 49.3 - 0.21[\text{Year}]$ ). The interaction term between site and year was not significant, indicating that the slopes were not significantly different.

**Growth rate.**—Mean growth rate in SVL was greater for iguanas from the feeding beach than for iguanas from the rest of Leaf Cay ( $1.03 \pm (\text{SE}) 0.05 \text{ cm yr}^{-1}$  [range,  $-0.4$ – $3.75 \text{ cm yr}^{-1}$ ;  $n = 232$ ] versus  $0.26 \pm 0.05 \text{ cm yr}^{-1}$  [range,  $-0.9$ – $1.75 \text{ cm yr}^{-1}$ ;  $n = 83$ ];  $F_{1,309} = 133.0$ ,  $P < 0.0001$ ). Overall, males grew significantly faster than females ( $1.14 \pm 0.07 \text{ cm yr}^{-1}$  [ $n = 162$ ] versus  $0.49 \pm 0.04 \text{ cm yr}^{-1}$  [ $n = 153$ ];  $F_{1,309} = 72.6$ ,  $P < 0.0001$ ). There was a significant sex by site interaction: the effect of the feeding beach was greater in males than in females (Table 1;  $F_{1,309} = 23.8$ ,  $P < 0.0001$ ). For all iguanas, growth rate declined with mean individual SVL ( $F_{1,309} = 30.7$ ,  $P < 0.0001$ ). There was a significant sex by mean SVL interaction ( $F_{1,309} = 14.9$ ,  $P = 0.0001$ ), with females reaching asymptotic growth at smaller sizes than males.

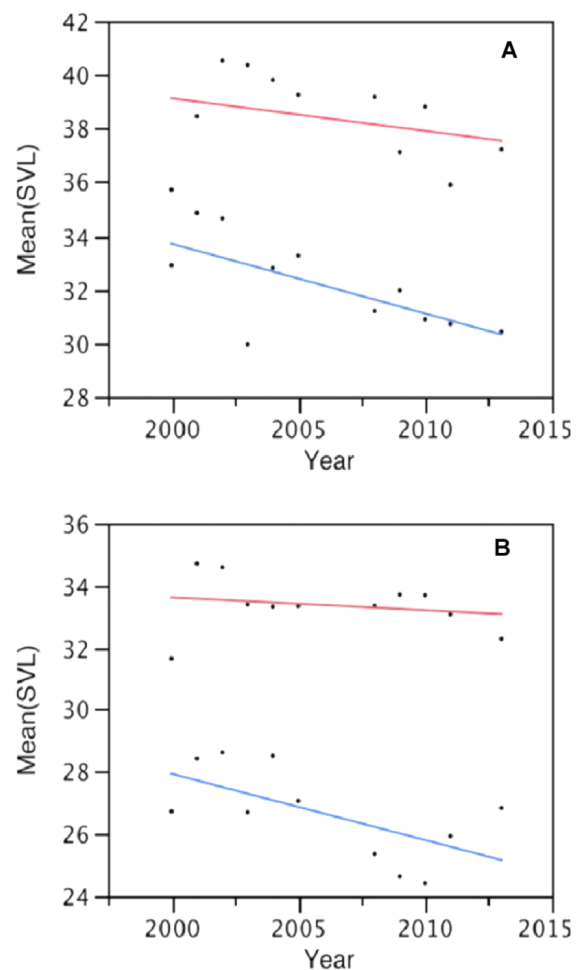


FIGURE 3. Mean snout-vent length (SVL in cm) of the largest (A) male and (B) female *Cyclura cychlura inornata* for yearly samples on Leaf Cay, The Bahamas, from 2000 to 2013 for iguanas from the feeding beach (red) and the rest of the cay (blue).

**TABLE 1.** Mean growth rates in snout-vent length (SVL) and body mass for male and female *Cyclura cyclura inornata* from the feeding beach and the rest of Leaf Cay, The Bahamas. Means are given  $\pm$  1 SE. Sample size (*n*) is given in parentheses.

	Feeding beach	Rest of cay
SVL		
Male	1.50 $\pm$ 0.07 cm yr <sup>-1</sup> (114)	0.29 $\pm$ 0.06 cm yr <sup>-1</sup> (48)
Female	0.57 $\pm$ 0.04 cm yr <sup>-1</sup> (118)	0.22 $\pm$ 0.07 cm yr <sup>-1</sup> (35)
BM		
Male	184.3 $\pm$ 14.4 g yr <sup>-1</sup> (104)	-10.6 $\pm$ 18.8 g yr <sup>-1</sup> (32)
Female	32.5 $\pm$ 4.8 g yr <sup>-1</sup> (104)	-7.5 $\pm$ 11.4 g yr <sup>-1</sup> (26)

Mean BM growth rate was much greater in iguanas from the feeding beach than iguanas from other areas, where BM change was negative (i.e., lost mass over time) on average (108.4  $\pm$  7.3 g yr<sup>-1</sup> [*n* = 208] versus -9.2  $\pm$  13.9 g yr<sup>-1</sup> [*n* = 58];  $F_{1,262} = 55.7$ ,  $P < 0.0001$ ). Overall, males gained mass faster than females (138.5  $\pm$  10.7 g yr<sup>-1</sup> [*n* = 136] versus 24.5  $\pm$  11.6 g yr<sup>-1</sup> [*n* = 130];  $F_{1,262} = 22.3$ ,  $P < 0.0001$ ). There was a significant sex by site interaction such that there was no significant difference in BM growth rate in females between the feeding beach site and the rest of the cay, whereas there was a larger difference for males from the two locations (Table 1;  $F_{1,262} = 24.3$ ,  $P < 0.0001$ ).

For males, logSVL was greater for iguanas from the feeding beach than the rest of the cay (Site effect:  $F_{1,408} = 35.4$ ,  $P < 0.0001$ ). LogSVL increased linearly with logAge ( $F_{1,408} = 601.6$ ,  $P < 0.0001$ ). There was a significant interaction between logAge and site such that males from the feeding beach showed a greater increase in body size as they aged compared to males from the rest of Leaf Cay (Fig. 4A; site  $\times$  logAge effect:  $F_{1,408} = 18.9$ ,  $P < 0.0001$ ;  $\log\text{SVL}_{\text{feeding beach}} = 0.96 + 0.46[\log\text{Age}]$ ,  $n = 365$ ;  $\log\text{SVL}_{\text{rest of Leaf Cay}} = 1.06 + 0.32[\log\text{Age}]$ ,  $n = 47$ ).

Female iguanas from the feeding beach had a greater mean logSVL compared to females from the rest of the cay (Site effect:  $F_{1,464} = 59.9$ ,  $P < 0.0001$ ). LogSVL increased linearly with logAge ( $F_{1,464} = 1108.1$ ,  $P < 0.0001$ ). There was a significant interaction between logAge and site such that females from the feeding beach showed a greater increase in body size as they aged compared to females from the rest of Leaf Cay (Fig. 4B; site  $\times$  logAge effect:  $F_{1,464} = 9.2$ ,  $P = 0.0026$ ;  $\log\text{SVL}_{\text{feeding beach}} = 1.06 + 0.32 \log\text{Age}$  [*n* = 396];  $\log\text{SVL}_{\text{rest of Leaf Cay}} = 1.08 + 0.27 \log\text{Age}$  [*n* = 72]).

**TABLE 2.** Estimates of body condition (residuals of logBM on logSVL regression and Fulton's K) for resident male and female *Cyclura cyclura inornata* from the feeding beach and the rest of Leaf Cay, The Bahamas. Means are given  $\pm$  1 SE. Sample size (*n*) is given in parentheses.

	Males		Females	
	Feeding Beach (114)	Rest of Cay (48)	Feeding Beach (118)	Rest of Cay (35)
Residuals	0.023 $\pm$ 0.012	-0.056 $\pm$ 0.011	0.009 $\pm$ 0.006	-0.029 $\pm$ 0.012
Fulton's K	0.042 $\pm$ 0.001	0.034 $\pm$ 0.001	0.036 $\pm$ 0.001	0.033 $\pm$ 0.001

**Body condition.**—In general, iguanas from the feeding beach on Leaf Cay weighed more at a given body length than iguanas from the other parts of the cay. Male iguanas from the feeding beach had significantly greater logSVL–logBM residuals ( $F_{1,159} = 15.8$ ,  $P < 0.0001$ ) and Fulton's K values ( $F_{1,159} = 16.2$ ,  $P < 0.0001$ ) than males from the rest of Leaf Cay (Table 2). Females from the feeding beach had greater mean logSVL–logBM residuals than did females from the rest of Leaf Cay (Table 2;  $F_{1,150} = 8.7$ ,  $P = 0.0037$ ). Fulton's K for females was also significantly greater on the feeding beach than on the rest of Leaf Cay (Table 2;  $F_{1,150} = 5.8$ ,  $P = 0.017$ ).

**Sex ratio.**—The mean proportion of captures that were males for the feeding beach site was 0.46  $\pm$  0.01 and for the rest of Leaf Cay was 0.50  $\pm$  0.04. For the vast majority of our surveys, the capture sex ratio did not differ significantly from 1:1 for either the feeding beach or the rest of Leaf Cay (Table 3). The proportion of captures that were male did not differ between the feeding beach and the rest of the cay (paired *t*-test on proportion males in each survey:  $t_{10} = 1.3$ ,  $P = 0.24$ ).

The proportion of captures that were male on the feeding beach tended to increase but this trend was not significant ( $n = 11$ ,  $r^2 = 0.23$ ,  $P = 0.13$ ). For the rest of Leaf Cay, there was no relationship between the survey year and the proportion of captured iguanas that were male ( $n = 11$ ,  $r^2 = 0.026$ ,  $P = 0.63$ ).

**Demography.**—The mean number of captures per individual was 4.80 for males on the feeding beach, 5.61 for females on the feeding beach, 3.27 for males from the rest of the cay, and 2.92 for females from the rest of the cay. The proportion of total captures that came from the feeding beach did not change over the course of the study (mean = 0.83  $\pm$  0.02;  $n = 11$ ,  $r^2 = 0.18$ ,  $P = 0.20$ ).

Annual survival rates did not differ for males or females between the feeding beaches and the rest of the cay (Table 4;  $t_9 = -0.28$ ,  $P = 0.79$ ). Capture probabilities for both males and females were higher on the feeding beach than on the rest of the cay (Table 5;  $t_9 = -1.7$ ,  $P = 0.11$ ).

**DISCUSSION**

Human interactions, presumably as a direct result of supplemental feeding, have apparently had significant impacts on size, growth, and body condition (but not demography) of iguanas on Leaf Cay. From 2000 through 2013, there has been a decrease in maximum body size in both females and (especially) males. We hypothesize that this decline is in large part due to removal of large, and potentially more aggressive and dangerous males, by tour operators or poachers. A shift in the sex ratios from male-dominated to equality on Leaf Cay over a similar period of time also supports this hypothesis (see Smith and Iverson 2006). This is further corroborated by our

**TABLE 3.** Number of resident males and females of Allen Cays Iguanas captured on the feeding beach and the rest of the cay for each survey on Leaf Cay, The Bahamas. \*indicates the observed sex ratio was significantly different from 1:1.

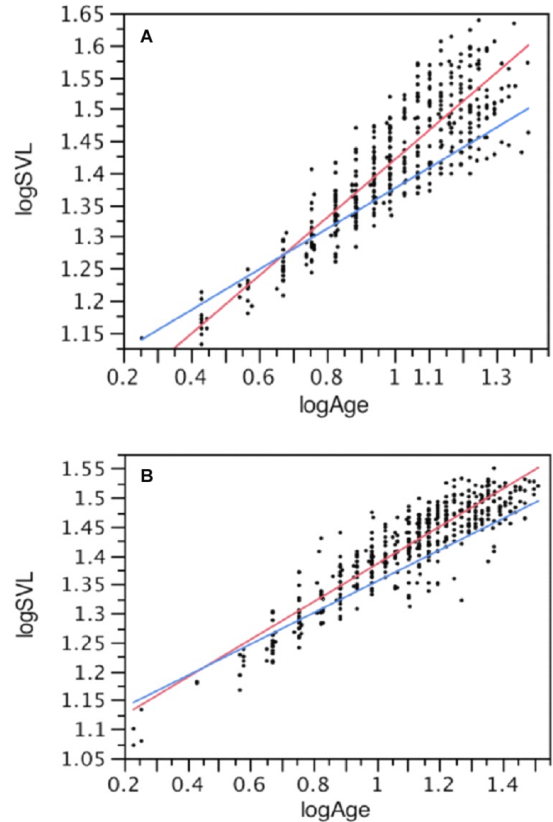
Year	Feeding beach		Rest of Leaf Cay	
	Males	Females	Males	Females
2000	43	62	4	7
2001	73	102*	42	25*
2002	83	113*	41	38
2003	62	63	11	10
2004	75	87	19	25
2005	56	72	14	13
2008	63	68	14	13
2009	50	60	3	8
2010	65	56	8	7
2011	44	55	9	3
2013	41	49	10	10

**TABLE 4.** Annual survival estimates for male and female *Cyclura cychlura inornata* from the feeding beach and the rest of Leaf Cay, The Bahamas. Estimates are given  $\pm$  1 SE; \*indicates SE < 0.0001.

Interval	Males		Females	
	Feeding beach	Rest of cay	Feeding beach	Rest of cay
2001–2002	1.000*	1.000*	1.000*	1.000*
2002–2003	0.999 $\pm$ 0.032	1.000*	0.973 $\pm$ 0.026	0.872 $\pm$ 0.094
2003–2004	0.830 $\pm$ 0.050	0.838 $\pm$ 0.118	0.956 $\pm$ 0.033	1.000*
2004–2005	0.919 $\pm$ 0.052	0.925 $\pm$ 0.165	0.884 $\pm$ 0.043	0.683 $\pm$ 0.131
2005–2008	0.907 $\pm$ 0.024	1.000*	0.940 $\pm$ 0.018	1.000*
2008–2009	0.909 $\pm$ 0.047	1.000*	0.997 $\pm$ 0.027	0.726 $\pm$ 0.242
2009–2010	0.905 $\pm$ 0.054	0.406 $\pm$ 0.109	0.997 $\pm$ 0.057	0.682 $\pm$ 0.276
2010–2011	0.822 $\pm$ 0.071	1.000*	0.862 $\pm$ 0.087	1.000*

**TABLE 5.** Capture probabilities for resident male and female *Cyclura cychlura inornata* from the feeding beach and the rest of Leaf Cay, The Bahamas. Estimates are given  $\pm$  1 SE.

Year	Males		Females	
	Feeding beach	Rest of cay	Feeding beach	Rest of cay
2000	0.971 $\pm$ 0.028	0.750 $\pm$ 0.216	0.933 $\pm$ 0.032	0.750 $\pm$ 0.153
2001	0.862 $\pm$ 0.043	0.865 $\pm$ 0.056	0.879 $\pm$ 0.034	0.769 $\pm$ 0.083
2002	0.738 $\pm$ 0.054	0.250 $\pm$ 0.065	0.627 $\pm$ 0.051	0.295 $\pm$ 0.086
2003	0.851 $\pm$ 0.046	0.380 $\pm$ 0.093	0.862 $\pm$ 0.039	0.622 $\pm$ 0.103
2004	0.738 $\pm$ 0.060	0.353 $\pm$ 0.090	0.762 $\pm$ 0.050	0.524 $\pm$ 0.125
2005	0.857 $\pm$ 0.050	0.353 $\pm$ 0.090	0.761 $\pm$ 0.050	0.306 $\pm$ 0.104
2008	0.697 $\pm$ 0.061	0.101 $\pm$ 0.050	0.719 $\pm$ 0.053	0.333 $\pm$ 0.142
2009	0.843 $\pm$ 0.054	0.372 $\pm$ 0.130	0.624 $\pm$ 0.063	0.333 $\pm$ 0.148
2010	0.763 $\pm$ 0.073	0.496 $\pm$ 0.140	0.678 $\pm$ 0.076	0.200 $\pm$ 0.115



**FIGURE 4.** Growth rate of *Cyclura cychlura inornata* on Leaf Cay, The Bahamas, based on snout-vent lengths (SVL in cm) at known ages. Males (top) and females (bottom) at the feeding beach (red) and the rest of the cay (blue).

discovery of large iguanas on at least six cays (up to 60 km distant) that were initially marked as residents on Leaf Cay. The decline of body size in iguanas on other parts of the island may be the result of the larger individuals there relocating to the feeding beach. However, it may also be the consequence of the population approaching carrying capacity or a long-term trend in some other factor (e.g., climate, primary productivity). One potential test of these hypotheses would be to examine these patterns on the much less visited nearby U Cay.

The feeding of iguanas by tourists appears to increase growth in the iguanas on Leaf Cay and also to improve their body condition. The larger body size of females from the feeding beach also likely increased their reproductive output since clutch size and reproductive frequency are positively related to female body size (Iverson et al. 2004a). Considering only these traits, one might argue that supplemental feeding by tourists has had a positive impact on the iguanas on Leaf Cay. However, other studies on the effects of ecotourism on the *C. cyclura inornata* on Leaf Cay suggest negative impacts on the individual iguanas. For example, the items consumed by iguanas on the Leaf Cay beach contained such things as trash and non-native foods, as well as sand (Hines 2011). One consequence of the altered diet was the consumption of foods with higher water content, resulting in hardened feces (Hines 2011), especially if such foods are consumed with sand (see Fig. 1 in Knapp et al. 2013), that may cause cloacal prolapse and possibly death (Hines et al. 2010).

In addition, *C. cyclura inornata* from Leaf Cay are less wary of humans than other islands where they are not fed (Hines 2011), potentially making it easier to poach these iguanas. Furthermore, large iguanas on the feeding beach, especially males, may also become more aggressive as they become entrained to human presence (pers. obs.), thus making them a threat to ecotourists, and potentially subject to removal by tour operators or poachers. These iguanas on Leaf Cay and other visited cays also showed no differences in hormonal stress responses to those from islands not visited by tourists (Knapp et al. 2013). Romero and Wikelski (2002) also found no difference in stress hormone levels between Galápagos Marine Iguanas (*Amblyrhynchus cristatus*) from areas visited by humans and areas not visited by humans (but see French et al. 2010 who found increased stress hormone levels in *A. cristatus* in visited populations compared to non-visited populations). Iguanas on Leaf Cay and other visited cays had increased endoparasite loads and more loose feces compared to those on cays not regularly visited by humans (Knapp et al. 2013). Fed iguanas also had higher blood glucose levels (presumably due to an artificial diet high in sugar), higher uric acid levels in the blood (presumably due to unnatural consumption of animal protein), and higher serum cholesterol and triglycerides (males only) (Knapp et al. 2013). Supplemental feeding has been shown to increase testosterone in lizards (e.g., *Sceloporus graciosus*, Ruiz et al. 2010), which could have

implications for aggression and other aspects of lizard behavior. Thus, while individuals may grow faster as a consequence of feeding by tourists, other aspects of their biology appear to be negatively affected, even though the consequences may be delayed for many years.

One alternative explanation for many of our results is that the habitat and environmental conditions may be better on the feeding beach than the rest of the cay, independent of the feeding that is taking place on the island. While this is a possibility, we unfortunately did not start to monitor the capture locations of individual iguanas until tourist feeding on Leaf Cay had already increased. Thus, we have no direct evidence to address this issue. However, indirect evidence suggests a predominant role of supplemental feeding in explaining our results. First, survival rates did not significantly differ between the beach and the rest of the cay. Second, data comparing the diets, endoparasites, blood chemistry, and behavior of Leaf Cay iguanas to conspecifics on islands without feeding suggest a clear impact of the feeding on individual *C. cyclura inornata* (Hines 2011; Knapp et al. 2013). Third, it is our impression that habitat quality on Leaf Cay is variable, but this variation in quality is not systematically distributed such that the “better” habitat is associated with the feeding beach.

At this time, it is not clear how the mixed effects of ecotourist visits to Leaf Cay on individual iguanas described above will translate into long-term demographic responses. Based on the lack of significant differences in capture sex ratios between the feeding beach and the rest of the cay, as well as the lack of consistent differences in survivorship between these two areas, there appear to be limited demographic effects of supplemental feeding for these iguanas, at least so far. Given the long-lived nature of *Cyclura*, even our 13-year study may not be sufficiently long to detect impacts on the demography of this population. Continued monitoring of these long-lived lizards will be necessary to fully understand such impacts. In addition, continued monitoring of other populations of *C. cyclura inornata* on cays without high levels of human visitation are needed to help discern the true impacts of ecotourism on the Allen Cay Iguanas of Leaf Cay.

We echo the recommendations of Knapp et al. (2013) concerning supplemental feeding by tourists on Leaf Cay and other cays that support *Cyclura*. Namely, we do not recommend stopping tourist visits nor do we recommend a cessation of supplemental feeding. Rather, we encourage the tour operators to modify their feeding procedures, perhaps by changing the food that they provide the tourists (see Knapp et al. 2013). We also agree with Knapp et al. (2013) in calling for some cays or populations of *Cyclura* to be protected from extensive, organized tourist visits and supplemental feeding. Such protected cays and populations would allow comparisons to be made between fed and unfed populations, as well as a hedge in the event that the long-term effects of tourism and supplemental feeding endanger *Cyclura* populations.

## Smith and Iverson.—Effects of Tourism on the Allen Cays Iguana.

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### LITERATURE CITED

- Aplasca, A.C. 2013. Population genetics of the endangered insular Allen Cays Rock Iguana, *Cyclura cychlura inornata*. M.Sc. Thesis, Fordham University, New York City, New York, USA. 52 p.
- Arcese, P., and J.N.M. Smith. 1988. Effects of population density and supplemental food on reproduction in Song Sparrows. *Journal of Animal Ecology* 57:119–136.
- Boyle, S.A., and F.B. Samson. 1985. Effects of nonconsumptive recreation on wildlife: a review. *Wildlife Society Bulletin* 13:110–116.
- Cone, R.S. 1989. The need to reconsider the use of condition indices in fishery science. *Transactions of the American Fisheries Society* 118:510–514.
- Dempster, T., P. Sanchez-Jerez, D. Fernandez-Joven, J. Bayle-Sempere, R. Nilsen, P.-A. Bjørn, and I. Uglem. 2011. Proxy measures of fitness suggest coastal fish farms can act as population sources and not ecological traps for wild gadoid fish. [PLoS ONE 6\(1\):e15646](https://doi.org/10.1371/journal.pone.0015646). doi:10.1371/journal.pone.0015646
- Fedriani, J.M., T.K. Fuller, and R.M. Sauvajot. 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography* 24:325–331.
- French, S.S., D.F. DeNardo, T.J. Greives, C.R. Strand, and G.E. Demas. 2010. Human disturbance alters endocrine and immune response in the Galápagos Marine Iguana (*Amblyrhynchus cristatus*). *Hormones and Behavior* 58:792–799.
- Garber, S.D., and J. Burger. 1995. A 20-yr study documenting the relationship between turtle decline and human recreation. *Ecological Applications* 54:1151–1162.
- García-Berthou, E. 2001. On the misuse of residuals in ecology: testing regression residuals vs. analysis of covariance. *Journal of Animal Ecology* 70:708–711.
- Green, A.J. 2001. Mass/length residuals: measures of body condition or generators of spurious results? *Ecology* 82:1473–1483.
- Harrison, R.L. 1997. A comparison of Grey Fox ecology between residential and undeveloped rural landscapes. *Journal of Wildlife Management* 61:112–122.
- Hines, K.N. 2011. Effects of ecotourism on endangered Northern Bahamian Rock Iguanas (*Cyclura cychlura*). *Herpetological Conservation and Biology* 6:250–259.
- Hines, K.N., C.R. Knapp, T.T. Zachariah, J.B. Iverson, and G.R. Smith. 2010. *Cyclura cychlura inornata*. Paraphimoses and prolapsed cloaca. *Herpetological Review* 41:77–78.
- Iverson, J.B., S.J. Converse, G.R. Smith, and J.M. Valiulis. 2006. Long-term trends in the demography of the Allen Cays Rock Iguana (*Cyclura cychlura inornata*): human disturbance and density-dependent effects. *Biological Conservation* 132:300–310.
- Iverson, J.B., K.N. Hines, and J.M. Valiulis. 2004a. The nesting ecology of the Allen Cays Rock Iguana, *Cyclura cychlura inornata* in The Bahamas. *Herpetological Monographs* 18:1–36.
- Iverson, J.B., G.R. Smith, and L. Pieper. 2004b. Factors affecting long-term growth of the Allen Cays Rock Iguana in The Bahamas. Pp. 176–192 *In* Iguanas: Biology and Conservation. Alberts, A.C, R. Carter, W. Hayes, and E. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.
- Jakob, E.M., S.D. Marshall, and G.W. Uetz. 1996. Estimating fitness: a comparison of body condition indices. *Oikos* 77:61–67.

- Jessop, T.S., P. Smitsen, F. Scheelings, and T. Dempster. 2012. Demographic and phenotypic effects of human mediated trophic subsidy on a large Australian lizard (*Varanus varius*): meal ticket or last supper? [PLoS One 7\(4\):e34069](https://doi.org/10.1371/journal.pone.0034069). doi:10.1371/journal.pone.0034069
- Kangas, K., M. Luoto, A. Ihtola, E. Tomppo, and P. Siikamäki. 2010. Recreation-induced changes in boreal bird communities in protected areas. *Ecological Applications* 20:1775–1786.
- Knapp, C.R. 2004. Ecotourism and its potential impact on iguana conservation in the Caribbean. Pp. 290–301 *In* Iguanas: Biology and Conservation. Alberts, A.C, R. Carter, W. Hayes, and E. Martins (Eds.). University of California Press, Berkeley and Los Angeles, California, USA.
- Knapp, C.R., K.N. Hines, T.T. Zachariah, C. Perez-Heydrich, J.B. Iverson, S.D. Buckner, S.C. Halach, C.R. Lattin, and L.M. Romero. 2013. Physiological effects of tourism and associated food provisioning in an endangered iguana. *Conservation Physiology* 1:1–12.
- Orams, M.B. 2002. Feeding wildlife as a tourism attraction: a review of issues and impacts. *Tourism Management* 23:281–293.
- Polis, G.A., W.B. Anderson, and R.D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics* 28:289–316.
- Robb, G.N., R.A. McDonald, D.E. Chamberlain, and S. Bearhop. 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. *Frontiers in Ecology and the Environment* 6:476–484.
- Rodríguez-Prieto, I., and E. Fernández-Juricic. 2005. Effects of direct human disturbance on the endemic Iberian frog *Rana iberica* at individual and population levels. *Biological Conservation* 123:1–9.
- Romero, L.M., and M. Wikelski. 2002. Exposure to tourism reduces stress-induced corticosterone levels in Galápagos Marine Iguanas. *Biological Conservation* 108:371–374.
- Rose, M.D., and G.A. Polis. 1998. The distribution and abundance of coyotes: the effects of allochthonous food subsidies from the sea. *Ecology* 79:998–1007.
- Ruiz, M., S.S. French, G.E. Demas, and E.P. Martins. 2010. Food supplementation and testosterone interact to influence reproductive behavior and immune function in *Sceloporus graciosus*. *Hormones and Behavior* 57:134–139.
- Schulte-Hostedde, A.I., B. Zinner, J.S. Millar, and G.J. Hickling. 2005. Restitution of mass-size residuals: validating body condition indices. *Ecology* 86:155–163.
- Smith, G.R., and J.B. Iverson. 2006. Changes in sex ratio over time in the endangered iguana *Cyclura cyclura inornata*. *Canadian Journal of Zoology* 84:1522–1527.
- Stevenson, R.D., and W.A. Woods. 2006. Condition indices for conservation: new uses for evolving tools. *Integrative and Comparative Biology* 46:1169–1190.
- Walpole, M.J. 2001. Feeding dragons in Komodo National Park: a tourism tool with conservation complications. *Animal Conservation* 4:67–73.
- Wells, F.H., W.K. Lauenroth, and J.B. Bradford. 2012. Recreational trails as corridors for alien plants in the Rocky Mountains, USA. *Western North American Naturalist* 72:507–533.
- White, G.C., and K.P. Burnham. 1999. Program MARK: Survival estimation for populations of marked animals. *Bird Study* 46(Suppl.):120–138.



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