*Full Length Research Paper*

# Evaluating headstarting as a management tool: Post-release success of green iguanas (*Iguana iguana*) in Costa Rica

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**Headstarting has become a popular tool employed by wildlife managers to help animal species-specifically those lacking or providing minimal parental care-offset extinction. However, many researchers challenge the conservation value of headstarting and urge proponents to monitor headstarted individuals following release into the wild to evaluate the success of headstart programs. As part of an experimental headstarting program managed by the Iguana Verde Foundation in Costa Rica, we conducted a 1.5-month radiotelemetry study of 11 headstarted 2 year old green iguanas (*Iguana iguana*) following their release into the wild at the Gandoca-Manzanillo Wildlife Refuge. Headstarted iguanas were compared to their wild counterparts (two radiotelemetered and 18 opportunistically-encountered) with respect to changes in growth, arboreal microhabitat use, social aggregation, activity ranges and movements. Male and female headstarted iguanas exhibited similar behaviours and headstarted iguanas were similar to wild iguanas for most variables measured. Thus, the headstarted green iguanas were clearly capable of short-term (1.5-month) survival in the wild and their apparently normal behaviours reflected the suitable conditions under which they were raised. The results provide insight into the ecology of green iguanas and will help guide headstarting and reintroduction programs for iguanas at this location and endangered iguanas elsewhere.**

**Key words:** Captive-breeding, conservation, headstarting, home range, lizard, radiotelemetry, reptilian, spatial use.

## INTRODUCTION

Headstarting is a conservation technique in which young animals, either captive-bred or collected from the wild, are reared in captivity until they attain a larger size prior to release into the wild. Theoretically, this strategy bene-fits species that are especially vulnerable to predation and/or starvation during the early stages of life and hence may help increase survivorship and number of breeding pairs in the wild (Ferguson et al., 1982; Alberts, 2007). Conceptually, headstarting is limited to those species lacking or providing minimal parental care (e.g., amphibians and reptiles). Headstarting emerged as a measure to help offset nest predation and high death rate in hatchling sea turtles (Pritchard, 1979; Bowen et al., 1994; Klima and McVey, 1995). However, the theory, application and implementation of headstarting tech-niques have often been criticized, leading researchers to question their conservation value (Dodd and Siegel, 1991; Reinert, 1991; Wilson et al., 2004; Enneson and Litzgus, 2008). A major concern of critics is that headstarting will cause individuals to lose their fear of humans and other potential predators, lose the ability to adjust to natural food sources after extended periods in captivity, or expose wild populations to novel diseases

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and pathogens (Alberts et al., 2004). Critics further argue that headstarting, like other reintroduction programs, usually lacks adequate post-release monitoring, which is necessary to properly assess whether or not projects were successes or failures (Dodd and Siegel, 1991; Reinert, 1991; Seddon et al., 2007). Moreover, head-starting does not specifically address the original cause of the population decline and therefore may not result in the establishment of self-sustaining populations (Siegel and Dodd, 2000).

Despite criticisms and objections, headstarting has become a prominent and promising tool for conservation, enjoying success in the recovery plans of several threatened or endangered species, including at least one amphibian (*Lithobates chiricahuensis*, Sprankle, 2008), marine turtles (e.g., *Lepidochelys kempii*, Shaver, 2005) and freshwater turtles (e.g., *Emys marmorata*, Spinks et al., 2003). Headstarting has also benefited recovery efforts for many endangered iguanas, including the Anegada iguana (*Cyclura pinguis*, Bradley and Gerber, 2005), Mona Island iguana (*C. cornuta stejnegeri*, Garcia et al., 2007; Perez-Buitrago et al., 2008), Grand Cayman iguana (*C. nubila lewis,* Knapp and Hudson, 2004), Cuban iguana (*C. n. nubila*, Alberts et al., 2004), Jamaican iguana (*C. collei*, Wilson et al., 2004) and Galapagos land iguana (*Conolophus subcristatus*, Cayot et al., 1994). Iguana hatchlings of both insular (Iverson, 2007; Pérez-Buitrago and Sabat, 2007; Knapp et al., 2010) and mainland (Harris, 1982; Van Devender, 1982; Laurie and Brown, 1990) species suffer much higher rates of mortality than adults.

Another iguana species now receiving international attention is the green iguana (*Iguana iguana*). This taxon is the most widely distributed lizard of the thirty-plus iguanas (Burghardt and Rand, 1985; Hollingsworth, 2004), occurring from Mexico southward to Brazil and Paraguay and also on many islands in the Caribbean, including Grenada, Curaçao, Trinidad and Tobago, St. Lucia, St. Vincent, Utila, Isla de Maiz Grande in Nicaragua and the Colombian islands of San Andres and Providencia (Censky et al., 1998; Savage, 2002). Green iguanas have also been introduced to southern Florida and Hawaii in the United States (Townsend et al., 2003) and have been reported as introduced pests in Puerto Rico (Engeman et al., 2005). Like other iguanids, green iguanas are largely herbivorous (Rand et al., 1990; van Marken, 1993). They are preyed upon by snakes, certain lizards, raptors and other birds and carnivorous mammals (Fitch et al., 1982; Savage, 2002). More problematic, they are subject to intense human exploitation (Eilers et al., 2002; TRAFFIC, 2008). In the past, a high reproductive potential helped this species withstand exploitation, but a combination of over-hunting and habitat fragmentation has accelerated their disappearance from areas of pre-vious abundance (Fitch et al., 1982). Despite legislative protection of green iguanas in most, if not all, of the countries where they occur, several wild green iguana populations are now endangered (Fitch et al., 1982;

Cohn, 1989; listed in Appendix II of CITES, the Con-vention on International Trade in Endangered Species of Wild Fauna and Flora) and in need of conservation action by wildlife managers.

Established in 2001, the Iguana Verde Foundation (IVF) undertook a headstart program to help offset a sharp decline in the green iguana population within the Gandoca-Manzanillo Wildlife Refuge (GMWR), located on the south Caribbean coast of Costa Rica. In 2001, rangers estimated the population in the refuge to be between 500 and 2,000 iguanas in an area of appro-ximately 5,011 hectares, and attributed the apparent decline to over-hunting of pregnant females and other adult iguanas for egg and meat consumption. Despite some initial setbacks, IVF succeeded in headstarting green iguanas in 2003 and released several headstarted iguanas into the wild in 2004 and 2005. In 2006, IVF was prepared to release more iguanas into the wild; however, aware of the possible negative effects of headstarting, IVF did not want to continue releasing iguanas without monitoring.

Here, the authors present the results of a 1.5-month post-release study aimed at determining if 2-year-old green iguanas headstarted at IVF are physically and behaviorally suited for successful release into the wild. The results of this study provide important ecological information for green iguanas in the GMWR during a portion of the wet season (June-August), and also provide insights into the efficacy of headstarting as a conservation tool for green iguanas and other endangered iguana species.

## MATERIALS AND METHODS

### Headstarting facility

The IVF is located on the Caribbean coast of Limon, Costa Rica, approximately 7 km south of Puerto Viejo, within the GMWR. The IVF initiated its headstarting program in 2001 with 10 adult wild green iguanas collected along the Sixaola River, within the GMWR, approximately 10 km from IVF. The iguana enclosure was ca. 150 m from the sea and ca. 50 m from the road connecting Puerto Viejo with Manzanillo. Captive green iguanas were raised within two linked enclosures (0.19 ha total), with a wall made of a 1.5-m tall wood framework and covered with stainless steel sheets (Figure 1). Several microhabitats that closely resembled the local iguana habitat setting were present within the enclosure, including: two sand mounds for nesting; various native shrubs and mature trees that served as sources of food and as basking and sleeping sites; and two separate man-made ponds (6 m × 3 m, 2 m deep). The enclosure was designed by IVF such that iguanas would be largely self-sustaining. Iguanas browsed primarily on vegetation within the enclosure, but supplemental vegetation was supplied every week or two. Since the first successful breeding year (2003), iguanas therein have yielded close to 100 - 300 hatchlings each year. Iguanas within the enclosure are subject to predation by raccoons (*Procyon lotor*, observed digging up nests during the present study) and possible predation of hatchlings and mature iguanas by opossums (*Didelphis virginiana*), common black-hawks (*Buteogallus anthracinus*), common basilisks (*Basiliscus vittatus*) and vine snakes (*Leptophis* sp.), all observed within or very close to the enclosure. Caretakers frequently remove potential predators

from the enclosure and maintain extra vigilance at night during the hatching period (April-July in enclosure). Black hawks are disturbed from nearby perching sites using sling shots aimed at nearby branches. Tree branches occasionally fall on the enclosure wall overnight and serve as temporary escape corridors for several iguanas. At the time of this study (July-August 2006), the enclosure was believed to house 100 - 200 mature (at least 2-year-old) iguanas and an estimated 100 hatchlings.

## Study site

The study site where headstarted iguanas were released and monitored was located 1.6 km east of IVF within the GMWR (09°38'N, 82°41'W). The GMWR occupies 9, 442 ha of sea and land in the southern Caribbean region of Costa Rica. The GMWR receives the least precipitation of the Caribbean region of Costa Rica, with a range of 2 - 2.5 m year-round. July - August and mid-November to mid-December are the rainiest periods. The mean temperature fluctuates between 22 and 27°C. The study site was approximately 250 m long (E - W) by 250 m wide (N - S) at its widest, totaling roughly 6.25 ha. Vegetation within the study site was best described as mixed primary and secondary tropical moist forest (Savage, 2002). Canopy trees reached 40 - 50 m tall, usually with wide crowns and 20 - 35 m of unbranched trunks. Shorter subcanopy trees had narrower crowns and reached up to 30 m high. The understory was characterized by mixed broad-leaved herbs, small palms, and ferns. The forest floor was mostly covered by damp leaf litter and a number of small depressions were periodically flooded up to 25 cm deep after strong rains. Representative trees included chilamate (*Ficus tonduzii*), javillo (*Hura crepitans*), guacimo colorado (*Luehea seemannii*) and jobo (*Spondias mombin*).

The site was chosen because wild green iguanas occurred in relatively high densities and it allowed for daily monitoring of both wild and headstarted iguanas. Suitable habitat into which the iguanas could emigrate extended well beyond the study site boundaries (Escobar, 2007). To avoid overcrowding, IVF had no intention of releasing additional iguanas into this property.

## Capture and marking

Six male and five female headstarted iguanas (2-year-olds) were captured within the enclosure on 3 - 4 July, using a thin, 6 m bamboo rod fitted with a noose at the tip. Males were distinguished from females by relative femoral pore size or head size and determined to be mature based on their body size (all ≥ 265 mm SVL; Dugan, 1982). Two wild male green iguanas were captured on 5 and 13 July (requiring 20 person-days of effort) by climbing 20 - 25 m into trees and using a 5-m aluminum collapsible noose. To facilitate identification in the field, the captive-raised and wild iguanas were painted with an F (female) or M (male) and a single-digit number on each dorsolateral side with white enamel (Hayes et al., 2000).

## Body size measurements and general health assessment

Before release, each iguana was weighed (± 0.01 kg) with a digital scale and the following body measurements were obtained to the nearest millimeter by collapsible wooden ruler or digital calipers: snout-vent length (SVL), tail length, head length, head width, and longest nuchal and dorsal spines. Iguanas were then inspected for open wounds, infections, number of missing toes and tail condition. The same measurements and general health assessment were conducted for all recaptured iguanas at the end of the study to evaluate foraging success, growth and injury in the wild.

## Radiotelemetry

The 11 headstarted IVF iguanas and two wild iguanas were fitted with radio-transmitters (model SOPB-2190, 6.0 - 7.0 g, 60 - 80 d battery life, Wildlife Materials Inc., Carbondale, Illinois) using the monofilament attachment method of Knapp and Owens (2005). Headstarted iguanas were randomly released at 50-m staggered intervals in the study area. Two of the 11 headstarted iguanas (M5 and F5) were released in swamp habitat. Wild iguanas were released at their original capture sites within the study area. Radio-tracking took place 4 - 6 times per week from 5 July - 25 August 2006. We located iguanas no more than once per day (with the exception of F1, which was tracked twice on July 10) using a Yaesu VR-500 receiver (100 kHz-1300 MHz; Vertex Standard USA, Cypress, California) and a two-element Yagi antenna. To minimize the possibility that iguanas could anticipate our approach, we also randomized the time and approach direction for all fixes. Upon each fix (location of iguana) we recorded date, time and GPS location (from a position directly beneath the iguana when in a tree). Actual sightings were not achieved for every GPS fix because of either the cryptic nature of green iguanas in trees or the visually-dense canopy. When iguanas remained in one location between successive fixes, we assigned the GPS location of the previous fix to minimize GPS measurement error.

## Arboreal microhabitat use and behaviours

For fixes resulting in actual sightings, we recorded the iguana's height in the tree using a Bushnell Sport 450 laser range-finder (Bushnell Corporation, Overland Park, Kansas) by standing directly under the iguana and bouncing the laser off the iguana or a nearby tree branch. We also recorded the tree species and measured the tree diameter at breast height using a diameter-at-breast-height tape. We relied on common tree names used by IVF and locals during the study to categorize tree species; however, some tree species were unknown to us and categorized as such. For each iguana sighting, we also recorded the activity (resting in sun, resting in shade, eating, fleeing, and fighting) in the tree. Iguanas were considered to be resting in sun if > 50% of body was in the sun; resting in shade if < 50% of body was in sun; eating if observed chewing on leaves or fruits; fleeing if moving away rapidly; and fighting if engaged in any ritualized agonistic behaviour. We also counted the number of additional iguanas in the same tree to give some indication of social behaviour in trees. The same data were collected when non-telemetered wild iguanas were incidentally encountered.

## Activity range analyses

We use the term "activity range" for headstarted iguanas instead of "home range," since iguanas presumably have yet to establish or perceive a defined home range (Figueroa et al., 2008). We used the Animal Movement Extension (AME; Hooge and Eichenlaub, 1997) in ArcView 3.3 (ESRI, Redlands, California) to estimate the seasonal (rainy season; Savage, 2002) activity range size using all fixes obtained from each iguana. We estimated the 100% minimum convex polygons (MCP: Jenrich and Turner, 1969) because they can be compared more readily to previous iguana studies (e.g., Dugan, 1982; Rand et al., 1989; Morales-Mávil et al., 2007). We also calculated 95% and core 50% fixed kernels (FK: Worton, 1995) because they are often regarded as more accurate estimators of activity range size (Seaman and Powell, 1996; Row and Blouin-Demers, 2006).

The 50% contours are reported, acknowledging their limitations (Powell, 2000), because they arbitrarily characterize the core area of use and provide potential insight into areas that may include

important resources to the animal (e.g., Dixon and Chapman, 1980). Default least-squares cross-validation was used to determine the smoothing factor for individual FK activity range sizes (Seaman and Powell, 1996; Knapp and Owens, 2005; Row and Blouin-Demers, 2006).

We also used AME to compute auto-correlation for each iguana, represented by Schoener's ratio ($t^2/r^2$; Swihart and Slade, 1985a). When autocorrelation exists ($t^2/r^2 < 2$), the relative distance moved between consecutive observations decreases, resulting in underestimates of activity range (Swihart and Slade, 1985b). Because M3 (headstarted) and M7 (wild) had only two unique fixes (fixes at different locations), they were not analyzed for MCP areas or Schoener's ratio.

### Movement analyses

We calculated the following movement variables:

1) Mean distance moved per day (mean m/day) over entire study = distance moved divided by number of days between successive fixes, averaged for all fixes (Gregory et al., 1987; Diffendorfer et al., 2005; Figueroa et al., 2008),
2) Dispersal distance = distance (m) from first to last location, and
3) Total distance traveled = sum of all distances moved (m) between successive fixes.

We applied circular statistics to analyze movement directionality using AME (Hooge and Eichenlaub, 1997) in ArcView 3.3 (ESRI, Redlands, California) to compute mean bearing, angular concentration (r), and Rayleigh's z (Zar, 1996). Circular statistics were not computed for iguana M3 (headstarted) and M7 (wild) because they had only two unique fixes (that is, fixes at different locations).

### Statistical analyses

As a general approach, we first compared male versus female headstarted iguanas, and then compared headstarted (sexes pooled) versus wild iguanas. Because radio-tracked iguanas were not always visually re-sighted, some observational data were too limited to compare differences between males and females. For continuous data involving multiple observations from a given animal, we always used the mean value from each iguana to avoid pseudoreplication (Hurlburt, 1984). For categorical data, however, our analyses included pseudoreplication and these were interpreted with its limitations in mind. We conducted statistical analyses using SPSS 12.0 for Windows (Statistical Package for the Social Sciences, Inc., Chicago, Illinois, 2003), with alpha = 0.05. Because assumptions of normality (Kolmogorov-Smirnov and Shapiro-Wilk tests) and homozygosity (Levene test) were virtually always met, we relied on parametric tests (Zar, 1996) for most analyses, including independent and one-sample $t$-tests and Pearson correlations ($r$). Results of parametric tests were essentially identical to those from corresponding nonparametric tests, giving us added confidence.

We also employed nonparametric Chi-square tests ($\chi^2$) for analyses of proportions (Conover, 1999). Because statistical significance is greatly affected by sample sizes, we also computed effect sizes, which are largely independent of sample size, dimensionless and more readily compared among different studies (Hojat and Xu, 2004). For pair-wise comparisons ($t$-tests), we relied on Cohens' $d$ using pooled standard deviation (Hojat and Xu, 2004), for which values > 0.8 are generally considered large (Cohen, 1988). For tests of proportions ($\chi^2$), we computed Phi ($\varphi$) for 2 × 2 and Cramer's $V$ for 2 × 3 contingency tables, with values > 0.5 deemed large (Cohen, 1988). Finally, we expressed bivariate correlations (Pearson's $r$) as coefficients of determination ($r^2$) with

values > 0.25 considered large (Cohen, 1988).

## RESULTS

### Body size differences and changes

Independent $t$-tests revealed no significant differences in initial SVL ($t = 0.50$, df = 7, $P = 0.63$, Cohen's $d = 0.33$) or mass ($t = 1.29$, df = 7, $P = 0.24$, Cohen's $d = 0.86$) between headstarted males and females (Table 1), though the large effect sizes suggested that males weighed more. Both male wild iguanas captured within the study site were larger and heavier than any of the headstarted iguanas (SVL: t = -8.27, df = 9, P < 0.001, Cohen's d = 6.46; mass: t = -6.87, df = 9, P < 0.001, Cohen's d = 7.59; Table 1). Mean (± 1 S.E.) increase in body mass of the headstarted (0.4 ± 4.6%) and wild (3.0 ± 9.0%) iguanas was statistically similar (t = 0.23, df = 5, P = 0.79, Cohen's d = 0.28; Table 1). Change in mass for headstarted iguanas varied from a loss of 1.7 g/day to a gain of 4.3 g/day. Change in mass for the two larger wild iguanas was a loss of 5.7 g/day and a gain of 9.1 g/day. Changes in SVL were not calculated because growth during the 1.5 - month period was less than the measurement error.

### Recapture success and survival

Though the wariness of iguanas to humans was not experimentally tested, headstarted iguanas showed no signs of habituation to humans or other problems associated with being raised in captivity. Iguanas exhibited violent fights when we attempted to capture them within the IVF enclosure, as well as in the wild at the conclusion of the study.

Seven iguanas, including five of the headstarted (three female and two male) and the two wild individuals released with transmitters, were recaptured at the end of the study (Table 1). Recapture success was 54% after a total effort of seven days (approximately 7 - 8 h daily), averaging one recapture per day. No attempt was made to recapture headstarted iguanas F5 and M5 due to the inaccessible swampy conditions in which they were released and remained for the duration of the study. There was no evidence of iguana mortality.

### Arboreal microhabitat use and behaviours

Independent t-tests revealed insubstantial differences between headstarted (N = 7 with resighting data) and wild (N = 18) iguanas with respect to iguana height in tree (t = -1.69, df = 23, P = 0.10, Cohen's d = 0.75), tree diameter (t = 0.41, df = 23, P = 0.69, Cohen's d = 0.18) and canopy cover (t = -0.62, df = 23, P = 0.54, Cohen's d =0.28). The mean (± 1 S.E.) height of iguanas when

**Table 1.** Radiotelemetry tracking details (Jul-Aug 2006) and green iguana (*Iguana iguana*) body size differences and changes.

| Iguana[a] | Fixes[b] | Survival days[c] | SVL before (mm)[d] | Mass before (kg) | Mass (kg)[e] after (%) |
|---|---|---|---|---|---|
| F1(HS) | 36 | 51 | 320 | 1.26 | 1.48 (+17) |
| F2(HS) | 34 | 29 | 320 | 1.27 | -- |
| F3(HS) | 33 | 46 | 295 | 0.95 | 0.87 (-9) |
| F4(HS) | 33 | 48 | 300 | 1.02 | 1.05 (+3) |
| M1(HS) | 35 | 50 | 330 | 1.51 | 1.47 (-3) |
| M2(HS) | 34 | 32 | 335 | 1.39 | -- |
| M3(HS) | 36 | 51 | 335 | 1.47 | 1.39 (-6) |
| M4(HS) | 34 | 45 | 265 | 0.90 | -- |
| M6(HS) | 35 | 51 | 319 | 1.28 | -- |
| M7(wild) | 34 | 51 | 480 | 4.86 | 4.57 (-6) |
| M8(wild) | 28 | 43 | 445 | 3.33 | 3.72 (+12) |
| All HS ♀♀ | 34 | 44 | 309 ± 7 | 1.13 ± 0.08 | 1.13±0.18 (3.7 ± 7.5) |
| All HS ♂♂ | 35 | 46 | 317 ± 13 | 1.31 ± 0.11 | 1.43 ±0.04 (-4.5 ± 1.5) |
| All HS | 35 | 45 | 313 ± 8 | 1.22 ± 0.07 | 1.25±0.12 (0.4 ± 4.6) |
| All Wild | 31 | 47 | 463 ± 18 | 4.10 ± 0.77 | 4.15±0.43 (3.0 ± 9.0) |

[a] F = female; M = male; HS = headstarted; wild = wild-captured. [b] Fixes = number of relocations during study; see Tables 2 and 3 for group summary statistics. [c] Estimated from iguana date of release to date of capture, last sighting, or last change of location; $\bar{x}$ ± 1 S.E. [d] Mass of iguana excluding transmitter; $\bar{x}$ ± 1 S.E. SVL after recapture not calculated because growth during the 1.5-month period was less than the measurement error. [e] Mass after recapture (and percent change in mass); $\bar{x}$ ± 1 S.E.

observed in trees was 22 m (± 2) for headstarted and 25 m (± 1) for wild iguanas. With the exception of M2 (headstarted) observed once on the ground, iguanas were always observed in trees between 15 m (M1; headstarted) and 33 m (M7; wild) above the ground. Diameter of trees used by headstarted and wild iguanas during the study averaged 55 cm (± 9) and 46 cm (± 4), respectively. An average canopy density of 78% (± 4.6%) and 82% (± 3.8%) was recorded from directly beneath headstarted and wild iguanas, respectively, which made it difficult for us to observe the subjects.

To compare use of tree species by headstarted ($N$ = 7 individuals) and wild iguanas ($N$ = 18 individuals, including two telemetered), we analyzed a sample of 56 observations ($N$ = 13 headstarted and 43 wild) from these 25 individuals. Because the data were categorical, this sample included pseudoreplication (up to 4 observations per individual). Iguanas were observed most often in *chilamate* (wild Figure 1, *F. tonduzii*; 66%) and *javillo* trees (sandbox tree, *H. crepitans*; 27%). Iguanas were observed only once in each of the remaining trees: *guacimo negro* (*Guazuma ulmifolia*), *jobo* (*S. mombin*), *sarua* (unknown Latin name) and *guavo* (unknown Latin name). In spite of pseudoreplication, which increases the likelihood of detecting a difference (Hurlbert, 1984), headstarted and wild iguanas were similarly distributed between the two most frequently used tree species ($x^2$ = 0.01, P = 0.93, $\varphi$ = 0.01). Because we did not measure relative abundance of tree species present at the study site, we could not test whether iguanas preferentially used specific tree species.

To examine behaviours, we analyzed 68 observations ($N$ = 18 headstarted and 50 wild) from the 25 individuals, which again included pseudoreplication. The majority of sightings involved iguanas resting in the sun (73.5%), with comparatively few resting in the shade (13.2%). Iguanas were observed feeding only on the *javillo* and *chilamate* trees, comprising 11.8% of observations. The remaining observation (1.5%) involved an iguana fleeing. Neither wild nor headstarted iguanas were observed exhibiting interspecific fighting behaviour during the radio-tracking study. Headstarted and wild iguanas exhibited similar frequencies of sunning, shading and feeding (headstarted: 64.7, 23.5 and 11.8%, respectively; wild: 78.0, 10.0 and 12.0%; $x^2$ = 2.03, Cramer's $V$ = 0.17, $P$ = 0.36, $N$ = 67). Both headstarted and wild iguanas were more often found in groups than singly. An independent $t$-test revealed no significant difference between head-started ($\bar{x}$ = 1.8 ± 0.49; $N$ = 7 with adequate data) and wild ($\bar{x}$ = 1.2 ± 0.10; $N$ = 18 presumably different individuals) iguanas in group size ($t$ = 1.76, df = 23, $P$ = 0.09, Cohen's $d$ = 0.78), though the large effect size suggested a somewhat greater affiliative tendency in headstarted iguanas. The largest group totaled 10 iguanas in a single tree, which included iguana F4 (headstarted) upon recapture at the end of the study.

**Figure 1.** Southeastern corner of the Iguana Verde Foundation headstart facility for green iguanas (*Iguana iguana*), illustrating the enclosure wall and vegetation within the enclosure.

**Table 2.** Activity ranges and movement data for headstarted male and female green iguanas (*Iguana iguana*).

| Dependent variable | Males | | | Females | | | Significance[a] | | |
|---|---|---|---|---|---|---|---|---|---|
| | *N* | $\bar{x}$ ± 1 S.E. | Range | *N* | $\bar{x}$ ± 1 S.E. | Range | *t* | *P* | *d* |
| Fixes | 5 | 34.8±0.4 | 34-36 | 4 | 34.0±0.7 | 33-36 | 1.06 | 0.32 | 0.71 |
| Moves | 5 | 8.0±1.6 | 2-11 | 4 | 6.0±0.6 | 5-7 | 1.07 | 0.32 | 0.72 |
| MCP100 (ha) | 4 | 0.46±0.21 | 0.04-1.06 | 4 | 0.38±0.19 | 0.09-0.93 | 0.30 | 0.78 | 0.21 |
| FK95 (ha) | 5 | 0.57±0.35 | 0.003-1.93 | 4 | 1.01±0.67 | 0.13-3.00 | 0.62 | 0.55 | 0.42 |
| FK50 (ha) | 5 | 0.05±0.03 | 0.001-0.15 | 4 | 0.15±0.09 | 0.02-0.43 | 1.12 | 0.30 | 0.75 |
| $t^2/r^2$ | 4 | 0.44±0.17 | 0.24-0.94 | 4 | 0.17±0.03 | 0.08-0.23 | 1.46 | 0.20 | 1.03 |
| Mean m/day | 5 | 6.1±1.7 | 0.8-10.0 | 4 | 5.0±1.4 | 2.6-8.7 | 0.45 | 0.66 | 0.30 |
| Dispersal (m) | 5 | 76±29 | 24-154 | 4 | 113±47 | 17-238 | 0.70 | 0.51 | 0.47 |
| Total distance (m) | 5 | 286±77 | 36-458 | 4 | 234±64 | 114-401 | 0.50 | 0.63 | 0.34 |
| Bearing | 4 | 184±39 | 133-298 | 4 | 163±42 | 58-237 | 0.38 | 0.72 | 0.26 |
| r | 4 | 0.21±0.04 | 0.09-0.28 | 4 | 0.35±0.11 | 0.04-0.53 | 1.19 | 0.28 | 0.84 |
| Raleigh's *z* | 4 | 0.49±0.19 | 0.06-0.85 | 4 | 0.92±0.41 | 0.01-1.69 | 0.96 | 0.37 | 0.68 |

[a] Significance includes independent *t*-test results (*t* and *P*) and Cohen's *d* effect sizes. All terms are defined in the methods section.

### Activity ranges and movements

Activity range and movement data are shown in Tables 2 and 3. Each of the 11 iguanas analyzed (9 headstarted; 2 wild) provided 28 - 36 fixes ($\bar{x}$ = 34), with 2-11 ($\bar{x}$ = 6; 17.6% of fixes) actual moves (number of fixes where in the animal changed location). Iguanas were visually detected on 26 of 372 fixes (7%). Among headstarted iguanas, independent *t*-tests indicated relatively minor differences (all p > 0.20; Cohen's *d* = 0.21-1.03) between sexes for activity range estimators (100% MCP, 95% FK, and 50% FK), movement variables (mean m/day, dispersal distance and total distance), autocorrelation values ($t^2/r^2$) and circular statistics (mean bearing,

**Table 3.** Activity ranges and movement data for headstarted versus wild-captured green iguanas (*Iguana iguana*).

| Dependent variable | Headstarted | | | Wild-captured | | | Significance | | |
|---|---|---|---|---|---|---|---|---|---|
| | N | $x \pm 1$ S.E. | Range | N | $x \pm 1$ S.E. | Range | t | P | d |
| Fixes | 9 | $34.4 \pm 0.4$ | 33 - 36 | 2 | $31.0 \pm 3.0$ | 28 - 34 | 2.49 | 0.03 | 1.95 |
| Moves | 9 | $7.1 \pm 0.9$ | 2 - 11 | 2 | $3.0 \pm 1.0$ | 2-4 | 1.96 | 0.08 | 1.53 |
| MCP100 (ha) | 8 | $0.42 \pm 0.13$ | 0.09 - 1.06 | 1 | 0.14 | -- | 0.72 | 0.50 | -- |
| FK95 (ha) | 9 | $0.76 \pm 0.34$ | 0.003 - 2.99 | 2 | $0.29 \pm 0.29$ | 0.001 - 0.57 | 0.63 | 0.55 | 0.49 |
| FK50 (ha) | 9 | $0.09 \pm 0.04$ | 0.001 - 0.43 | 2 | $0.04 \pm 0.04$ | 0.000 - 0.08 | 0.51 | 0.62 | 0.40 |
| $t^2/r^2$ | 8 | $0.31 \pm 0.10$ | 0.08 - 0.94 | 1 | 0.20 | -- | 0.37 | 0.72 | -- |
| Mean m/day | 9 | $5.6 \pm 1.1$ | 0.8 - 10.0 | 2 | $2.5 \pm 1.7$ | 0.8 - 4.2 | 1.28 | 0.23 | 1.00 |
| Dispersal (m) | 9 | $92 \pm 25$ | 17 - 238 | 2 | $47 \pm 47$ | 0 - 94 | 0.78 | 0.46 | 0.61 |
| Total distance (m) | 9 | $263 \pm 49$ | 36 - 458 | 2 | $108 \pm 68$ | 40 - 176 | 1.40 | 0.20 | 1.09 |
| Bearing | 8 | $173 \pm 75$ | 58 - 298 | 1 | 303 | -- | 1.63 | 0.15 | -- |
| r | 8 | $0.28 \pm 0.06$ | 0.04 - 0.53 | 1 | 0.22 | -- | 0.32 | 0.76 | -- |
| Raleigh's z | 8 | $0.70 \pm 0.22$ | 0.01 - 1.69 | 1 | 0.15 | -- | 0.83 | 0.43 | -- |

[a] Significance includes independent *t*-test results (*t* and *P*) and Cohen's *d* effect sizes. All terms are defined in the *Methods* section.

angular concentration and Rayleigh's *Z*). Headstarted iguanas tended to occupy larger activity ranges and move over greater distances than wild iguanas, but the differences were moderate (all p > 0.15; Cohen's *d* = 0.40 - 1.09). The 95% FK activity range was 1.8-fold and 2.1-fold larger than the 100% MCP activity range for headstarted and wild iguanas, respectively. The core area (50% FK) represented 11.8 and 13.8% of the 95% FK activity range in headstarted and wild iguanas, respectively. Autocorrelation values were all well below 2.0, ranging from 0.08 -0.94 ($\bar{x}$ = 0.29), indicating strong time-dependence between successive observations and likely underestimation of activity ranges (Swihart and Slade, 1985b). Movements were random in compass bearing rather than directional, since the Rayleigh's *z* value for every radio-tracked iguana was non-significant (all p > 0.05). Mean bearing for headstarted iguanas was southward (173˚), suggesting no tendency to return westward toward the rearing facility (ca. 270˚).

Pearson correlations (expressed as coefficients of determination) revealed that the three activity range variables, three movement variables, autocorrelation ($t^2/r^2$), and angular concentration were largely independent of body size (SVL and mass; $r^2$ = 0.00-0.26, all p > 0.11, N = 9-11) and number of fixes ($r^2$ = 0.00-0.21, all p > 0.22, N = 9-11). The three activity range estimators were positively correlated with each other (all $r^2 \geq 0.56$, p ≤ 0.020, N = 9-11). Two of these, 100% MCP and 95% FK, were positively correlated with all three movement distance variables ($r^2 \geq 0.46$, p ≤ 0.021, N = 9-11), whereas 50% FK was positively correlated with dispersal distance ($r^2$ = 0.75, p < 0.001, N = 11) and positively associated with m/day and total distance ($r^2$ = 0.34, p = 0.052, N = 11 and $r^2$ = 0.36, p = 0.059, N = 11, respectively; note the large effect sizes). All movement distance variables were also positively correlated with

each other (all $r^2 \geq 0.61$, p ≤ 0.004, N = 11). Autocorrelation ($t^2/r^2$) values were negatively but only moderately associated with the three activity ranges, dispersal distance and angular concentration ($r^2$ = 0.13-0.33, p = 0.11-0.34, N = 9). Finally, angular concentration was positively but rather weakly associated with the three activity ranges and dispersal distance ($r^2$ = 0.08-0.22; p = 0.20-0.45, N = 9).

## DISCUSSION

In this study, we relied on radiotelemetry to evaluate the success of 2-year-old headstarted green iguanas released into the wild by comparing their behaviours and habitat use to those of non-captive-reared iguanas. Because the behavioural and ecological variables analyzed were largely similar for the male and female headstarted iguanas, we felt justified in pooling the two sexes for comparison to the two radio-telemetered wild iguanas and other wild iguanas observed incidentally. More importantly, the analyses revealed considerable similarity between headstarted and wild iguanas, suggesting that the headstarting approach used by the IVF should succeed in augmenting depleted iguana populations in the wild. The sample size for radio-tracked iguanas (N = 11; 9 headstarted, 2 wild) was within the range of other published studies of headstarted rock iguanas (*Cylcura* spp.; García et al., 2007: N = 8; Lewis et al., 2008: N = 6) and of green iguana home ranges (Dugan, 1982: N = 18 large adults; Rand et al., 1989: N = 5; Morales-Mávil et al., 2007: N = 8). The sample size for wild iguanas was substantial for ethological comparisons (arboreal microhabitat use and behaviors; N = 18), but the number actually tracked with transmitters (N = 2) was unfortunately small for the activity range and movement

comparisons. Nevertheless, effect sizes for most comparisons were small to moderate. Some differences would be expected given the large number of comparisons made.  In the sections that follow, we address the dependent measures that support our conclusions.

**Growth and survival**

Both headstarted and wild iguanas averaged a net gain in weight during the 1.5 months of tracking, with a negligible difference between the groups. Body size of the headstarted iguanas matched closely those of similar-aged wild green iguanas in Costa Rica (Van Devender, 1982), suggesting suitable rearing conditions within the IVF headstarting enclosure. Wild iguanas would have been expected to grow < 1 cm in length during the mean 45-day tracking period (Van Devender, 1982), a change that was less than our measurement error for non-anesthetized lizards. Unfortunately, we could not find in the literature comparable rates for growth in mass (Baer et al., 1997, for a laboratory-based study), but the rates of change we measured were adequate to detect differences between groups over the study period had they existed.

Past studies of Jamaican iguanas (*C. collie*) suggested that, because of the high moisture content of commercially grown fruits and vegetables, feeding iguanas in captivity may predispose them to substantial water weight loss immediately upon release in the wild (Hudson, 2000; Lewis et al., 2008). Hudson (2000) further argued that using such highly palatable diets in captivity may slow down the ability of iguanas to adapt to feeding on native vegetation.

Although some headstarted iguanas in our study lost weight, it was small compared to weight losses observed in Jamaican iguanas (Hudson, 2000; Lewis et al., 2008). The headstarted iguanas within the *in-situ* enclosure at IVF benefited from being able to actively search and choose from a diet strictly composed of a variety of native plant choices. Hence, any possible weight losses related to diet may have been considerably reduced due to the husbandry methods used by IVF.

We found no evidence of mortality among our iguanas and suspect that survival was at or close to 100% during the 1.5-month tracking period.  Survival of our 2-year-old iguanas contrasted sharply with neonates at the same study site, which suffered 34.8 - 47.8% mortality within the first month after release (Knapp and Abarca, 2009). Headstarted Caribbean rock iguanas (*Cyclura* spp.) have generally fared well, with survival (generally under-estimated) ranging from 40 - 83% within the first 2 years (Alberts et al., 2004; Wilson et al., 2004; Bradley and Gerber, 2005; Pérez-Buitrago et al., 2008). With more predators on the continental mainland, one might expect higher mortality in our green iguana population,  but we were unable to assess this possibility (c.f., Knapp et al., 2010).

Many researchers often assume  that  radiotelemetry studies do not affect normal movement and behaviour of animals (Knapp and Owens, 2005; Knapp and Abarca, 2009; Weatherhead and Blouin-Demers, 2004). Compared to the wild iguanas, survival, growth, behaviour and movements of the headstarted iguanas might have been more affected by the transmitters for two reasons: the ratio of transmitter mass to body mass was greater for headstarted iguanas and, unlike the larger wild iguanas, some suffered abrasions from the monofilament attachment of the transmitters to the body (Escobar, 2007). However, the minor differences in quantitative measures between headstarted and wild iguanas suggest adequate tolerance and minimal impact of the transmitters. Moreover, Knapp and Abarca (2009) showed that transmitters up to 7.5% of body weight had minimal impact on growth and locomotor performance of neonates at our study site. Goodman et al. (2009) reviewed different telemetry attachment options, some of which they recommend instead of ours, which was based on Knapp and Owens (2005).

**Arboreal microhabitat use and behaviors**

Both headstarted and wild telemetered iguanas remained high in trees during this study, with the exception of headstarted iguana M2 (observed once fleeing on the ground and up a tree). However, telemetered iguanas likely descended to the ground for some of their longer movements. Green iguanas have been known to remain in tree tops from one day to several weeks, apparently because a single tree could meet all of an iguana's short-term requirements (food, thermoregulatory sites, and sleeping perches), with the iguana only rarely descending for basking, tree-to-tree movement, or escape from predators (Dugan, 1982). Iguana tree height preferences in this study (15 - 33 m) were similar to heights reported by Hirth (1963) at 6 - 25 m above the ground. However, iguanas in our study averaged higher perches (22 m headstarted, 25 m wild) than those reported in other studies; this may be a result of many of the trees in our study site being unbranched for at least 20 m. Although headstarted iguanas were raised within an enclosure where the tallest trees reached approximately 15 m, they experienced no obvious problems after release to the wild, quickly adjusting to the taller tree heights. This is important because the ability to remain high in trees, limiting time on or near the ground, protects iguanas from dogs on nearby properties and easy detection by human poachers. The frequency of behaviors (sunning, shading, and feeding) while in the trees was similar for headstarted and wild iguanas.

Although green iguanas are occasionally found alone, they are more commonly found in groups during the non-breeding season (Hirth, 1963; Dugan, 1982). Hirth (1963)

reported a maximum of four adult iguanas in a single group and Dugan (1982) reported groups of up to 10 iguanas of various ages in a single tree. Muñoz et al. (2003) reported an average of 1.5 iguanas/group in areas adjacent to swamp habitat and 2.5 iguanas/group in areas along rivers. In our study, although telemetered iguanas sometimes were observed alone (assuming we did not miss other iguanas in the tree), both headstarted and wild iguanas were more often found in groups ($\bar{x}$ = 2 individuals/group) than singly, and on one occasion in a group (~10 m from water source) as large as 10 individuals. More importantly, headstarted iguanas were observed on several occasions in the same tree with other wild iguanas, showing signs of proper social integration into the local population, which allowed them to take advantage of group benefits. Among the reasons suggested for group behaviour in iguanas are exploitation of a shared food source and better avoidance of predators (Hamilton, 1971; Gross and MacMillan, 1981; Auffenberg, 1982; Burghardt and Rand, 1985; Krakauer, 1995; Rivas and Levin, 2004). We suspect that iguanas within the GMWR tend to occur in groups more so to avoid predators rather than to exploit a food source, since suitable, non-utilized food trees were abundant within the study site.

**Activity range and movements**

Prior studies suggest that mature green iguanas (>260 mm) lead relatively sedentary lifestyles outside of the nesting season, confining their movements to small home ranges. Mean 100% MCP values have been reported at 0.18 ha (Dugan, 1982), 0.98 ha (Rand et al., 1989), and 0.79 ha (Morales-Mávil et al., 2007). The mean 100% MCP for all telemetered iguanas in our study outside of the breeding season was also small (0.39 ± 0.12 ha). Including our study, no sex differences have been reported. Green iguanas may occupy small home ranges relative to other iguanas because of the substantial vertical component to their habitat use. Because body size, generally corresponding to age and experience, can potentially affect home range size and movements (Pérez-Buitrago and Sabat, 2007), any differences in activity range and movements between the smaller headstarted and larger wild iguanas could have reflected an ontogenetic effect. However, we found no strong associations of body size with either activity range or movements. Among iguanas, scarcer food sources typically translate into larger home range sizes for iguanas because they have to travel longer distances to find food (Iverson, 1979; Rand et al., 1989; Pérez-Buitrago et al., 2007). Population density may also be important, with iguanas generally occupying larger home ranges at lower density (Pérez-Buitrago et al., 2007). The small activity range sizes observed in our study and absence of iguanas wandering outside of the study site

boundaries suggest an abundance of food sources within the study area and minimal competition from resident wild iguanas.

Correlation analyses suggested that iguanas which moved further (larger dispersal distance) and in a more directional manner (smaller angular concentration) had larger home range values and greater autocorrelation (lower $t^2/r^2$ values). Although, autocorrelation results in underestimates of activity range (Swihart and Slade, 1985b), it can be positively associated with home range size (Blundell et al., 2001; Figueroa et al., 2008) and may reflect directional movement as much as insufficient time between successive locations. Autocorrelation is seldom reported in iguana studies (for exceptions, Cyril, 2001; Goodman et al., 2005), so its effect on activity range estimates remains unclear, not just for iguanas but for amphibians and reptiles in general (Row and Blouin-Demers, 2006).

Although headstarted iguanas in our study integrated well with wild iguanas and appeared to behave normally, other headstarting studies with rock iguanas (*Cyclura*) have shown mixed results. Headstarted 8 - 20-month-old Cuban iguanas (*C. nubila*) appeared to behave normally after release, exhibiting growth, antipredator behaviours (approach distances), body temperatures and ectoparasite loads similar to wild iguanas (Alberts et al., 2004). Headstarted 3-year-old Mona Island iguanas (*C. c. stejnegeri*), in contrast, experienced growth comparable to wild iguanas, but all recaptures (25 of 62 released) were individuals that migrated (or "homed") from the release site back to the rearing facilities without establishing territories typical for adult wild iguanas (Pérez-Buitrago et al., 2008). Our headstarted iguanas showed no homing tendency. Headstarted Mona Island iguanas also occupied much larger home range sizes than wild hatchlings or adults (García et al., 2007; Pérez-Buitrago et al., 2007; Pérez-Buitrago and Sabat, 2007). Our headstarted iguanas showed a similar tendency for larger home ranges, but effect sizes (Cohen's *d* = 0.40-1.09) were much smaller than those for Mona Island iguanas (Cohen's *d* = 6.39 for 100% MCP of headstarted vs. wild adult iguanas). Headstarted Jamaican iguanas (*C. collei*) of unreported age remained near their release sites and established home ranges smaller in size than those reported for other *Cyclura* species, but all lost fairly substantial mass over 3.5 - 6.5 months of tracking (Lewis et al., 2008). The iguanas of the present study, on average, gained weight over the 1.5 months of tracking.

**Conclusion**

Our study suggests that iguanas headstarted at IVF rapidly adjusted to their new environments following release, exhibiting behaviours similar to their wild counterparts. Although we tracked these iguanas for only 1.5 months, we also suspect they were likely to survive

long term. Headstarting will no doubt continue to be used as more species become threatened by human activities. Critics will continue to give reasons for discontinuing such efforts and proponents will continue to advocate the many positive outcomes of such aggressive tools. However, this type of debate should encourage experimental development of new and better headstarting methods and monitoring techniques, ultimately providing wildlife managers with more options for helping species in peril.

## ACKNOWLEDGMENTS

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