

EFFECTS OF RADIO TRANSMITTER BURDENING ON LOCOMOTOR ABILITY AND SURVIVAL OF IGUANA HATCHLINGS

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ABSTRACT: We performed a two-part experiment in 2007 and 2008 to investigate the effects of externally affixed radio transmitters on the locomotor performance and survival of green iguana (*Iguana iguana*) hatchlings. Using sprint and climb speeds as locomotor performance variables, we tested in the laboratory the initial speed, maximum burst speed, and overall speed of iguana hatchlings affixed with radio transmitters of 2.5, 5.0, 7.5, 10.0, and 15.0% transmitter-to-body-mass (BM) ratios. We then released iguana hatchlings into a Costa Rican lowland forest to record the survival of free-ranging iguanas affixed with transmitters of 5.0, 7.5, and 10.0% transmitter to BM ratios. Sprint speeds were not reduced significantly with transmitters of up to 15.0% body mass. Climb speeds, however, were reduced for two of three performance variables at the 10% BM ratio. We found no differences in survival probabilities between telemetered treatment groups released into the forest. The probability of survival over two field seasons for telemetered iguanas ranged from 52.2–65.2% over a 24–30 day assessment period. For telemetered iguanas, percentage BM growth was significantly less for animals affixed with 10.0% BM transmitters than for control iguanas without transmitters. We suggest transmitter-to-body-mass ratios for cryptic arboreal lizard species should not exceed 7.5% based on lower climb performance in the laboratory and lower relative mass gain for free-ranging iguanas with $\geq 10.0\%$ BM transmitters. Because lizard life histories vary substantially, researchers should be proactive in evaluating the energetic expenditures, foraging strategies, and escape responses of focal species to minimize effects of transmitter and attachment techniques.

Key words: *Iguana iguana*; Lizard; Performance; Radiotelemetry

RADIO telemetry is an effective method for acquiring ecological information that can be used when designing and implementing wildlife management strategies, or for investigating hypothesis-driven research questions. An important assumption associated with telemetry studies is that the behavior of tagged individuals is representative of those in the population at large. However, this is not always the case, as studies from a variety of animals have reported adverse effects of radio transmitters, including decreased reproduction (Cotter and Gratto, 1995), reduced body mass (Tuytens et al., 2002), changes in behavior (Chipman et al., 2007), and reduced survivorship (Steenhof et al., 2006).

To ensure effective and ethically sound research, ecologists must be proactive in investigating the potential effects of research techniques and disseminating the information to their peers and wildlife managers (McMahon et al., 2007). Attempts to evaluate the effects of transmitters often have focused on non-squamates such as amphibians (e.g., Blomquist and Hunter, 2007), fish (e.g.,

Murchie et al., 2004), birds (e.g., Robert et al., 2006), and mammals (e.g., Moorhouse and Macdonald, 2005). To our knowledge, there have been no investigations to address experimentally the effects of externally affixed radio transmitters on lizards. This is particularly disconcerting because recent telemetry studies of lizards have focused on endangered taxa for which the effects of transmitter attachment must be weighed against the potential benefits of gaining information critical to conservation and management of imperiled species (Goodman et al., 2005, 2009; Knapp and Owens, 2005a). Moreover, data obtained from studies without knowledge of transmitter effects may be spurious and the resulting interpretations inaccurate.

Transmitter sizes and attachment techniques are a compromise between minimizing potential negative effects of carrying the transmitter and maximizing transmitter retention, range, and longevity. Wildlife researchers conducting telemetry studies on reptiles have been guided to date by an arbitrary 5–10% ratio of transmitter-to-body-mass recommendation (White and Garrott, 1990). Affixing appropriate-sized transmitters to large lizards

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is easier than with smaller lizards because there is less of a transmitter-to-body-mass constraint. However, most of the approximately 4700 species of lizards are small and only approximately 60 attain an adult body mass of over one kilogram. Additionally, crucial data are overlooked when investigating only adults of any species because relative survival of pre-reproductive individuals is a major determinant of population dynamics and life-history evolution (Civantos and Forsman, 2000). Therefore, it is important to determine the effects of transmitter burdening using small lizards to strengthen our ability to perform comprehensive science.

Using sprint and climb speeds as locomotor performance variables, the first objective of this study was to test the initial speed, maximum burst speed, and overall speed of green iguana (*Iguana iguana*) hatchlings affixed with radio transmitters ranging from 2.5–15.0% transmitter-to-body-mass ratios. These locomotor performance measures were chosen based on published reports of hatchling green iguana movements (Drummond and Burghardt, 1982; Henderson, 1974; Rivas and Levín, 2004) and common predators (Greene et al., 1978; Rivas et al., 1998; Van Devender, 1982). Dispersing green iguanas have a tendency to follow a terrestrial route before establishing themselves in shrubs and low trees. Therefore, sprint ability was tested because it benefits iguana hatchlings in circumstances in which a predator is actively foraging terrestrially or aerially (Christian and Tracy, 1981). Green iguanas also climb regularly through a complex vegetation matrix. Therefore, climbing performance was tested because it could affect the ability to escape predators as well as secure optimal feeding and retreat sites.

Intuitively, one can conclude that physical burdens pose some constraint on animal mobility. However, the importance of locomotor decrements in an ecological context is influenced by how shifts in locomotor ability translate into changes in vulnerability to predation. For example, some species may not depend upon speed to evade predation (e.g., Schwarzkopf and Shine, 1992). Thus, lowered performance in the laboratory is not an unfailling predictor of increased predation

under natural conditions. Therefore, the second objective of this study was to record the survival of free-ranging hatchling green iguanas affixed with transmitters ranging from 5.0–10.0% of their body mass.

MATERIALS AND METHODS

Performance trials were conducted at the Iguana Verde Foundation (IVF) located within the Gandoca-Manzanillo Wildlife Refuge (GMWR; 5013 terrestrial ha) on the south Caribbean coast of Costa Rica. The IVF has several natural iguana enclosures (up to 2000 m²) of mixed male and female age classes. Breeding and oviposition occurs naturally from January to June. In June, hatchling iguanas were captured by noose in the enclosures and housed in outdoor, screened cages (50 × 60 × 100 cm) with natural vegetation. Water was offered ad libitum and food supplemented daily with local flowers and twice weekly with shredded pumpkin. We recorded snout-vent length (SVL) and body mass (BM) at capture. All iguana hatchlings used in this study were between two and four weeks of age.

After the performance trials, a different subset of iguana hatchlings was released and radio tracked in the GMWR. The GMWR is characterized as a mixed primary and secondary lowland tropical moist forest with some areas of cleared understory. Canopy trees reach heights of 40–50 m whereas the understory is comprised of broad-leaved herbaceous species, dwarf palms, and ferns. Representative dominant plants species for the GMWR include *Ficus tonduzii*, *Hura crepitans*, *Luehea seemannii*, *Piper candelarianum*, and *Spondias mombin* (Hartshorn, 1983).

Laboratory Performance Trials

We investigated locomotor performance for green iguana hatchlings in June 2007 and 2008. In June 2007 we used treatment groups with transmitter to BM ratios of 2.5, 5.0, and 7.5% along with a control group without transmitters. In June 2008 we increased the range of transmitter to BM ratios by using 5.0, 10.0, and 15.0% treatment groups. Dummy transmitters (BD-2; Holohil Systems Ltd., Ontario, Canada) ranging from 0.4 to 2.4 g with 14 cm trailing antennas were affixed

anterior to the hind limbs on the dorsal side of the pelvic girdle with a 4 mm wide strip of duct tape. Different lengths of 20-gauge utility wire were rolled in a horizontal spiral and duct taped to the top of the transmitters to produce the correct transmitter to BM ratios for each treatment and each iguana.

We measured sprint speed using a 2 m long electronic raceway with a high-friction sandpaper substrate. The raceway measured 6.5 cm wide during the 2007 trials. We increased the width of the raceway to 9.5 cm in 2008 after post-evaluating sprint video files (used for documentation purposes) because in some trials the claws of sprinting individuals touched the walls of the raceway. Consequently, faster speeds in 2008 were most likely the result of the wider raceway (see Results). Laser beams with corresponding photocells placed every 50 cm and connected to an electronic clock recorded the time taken for lizards to cross each successive beam. The time elapsed between triggering two consecutive beams was recorded and expressed as cm s^{-1} for each interval. Immediately prior to sprinting, we placed hatchlings for 30 min in a thermal box heated to 34 C, which fell within the range of cloacal temperatures recorded for hatchlings captured within the outdoor enclosure at the IVF (C. Knapp, unpublished data). We then positioned lizards at the beginning of the raceway and induced them to run by tapping the tail with a paintbrush. Each run was scored as "good" or "poor" (Losos et al., 2002) based on lizards that cycled limbs rapidly or that moved limbs only partially and exerted suboptimal effort. Trials with poor ratings were eliminated from further analysis.

For each lizard, we recorded the initial speed over the first 50 cm segment of raceway to provide an index of acceleration (Miles, 2004), and potential ability to escape the initial strike of a predator. We also recorded the maximum speed over any 50 cm interval as an estimate of maximum burst speed. Speed over the entire raceway (overall speed) was calculated to measure the ability of hatchlings to maintain speed over a relatively longer distance. Lizards participated in all treatment trials, which were randomized for each lizard and measured on different days.

Each hatchling was sprinted three times consecutively for each treatment group, with ≥ 15 min spent in the thermal box between trials. In some cases, when equipment failed or an animal was especially uncooperative, we re-ran an individual immediately. Thus, some iguanas performed an extra locomotor trial. Following at least one trial per treatment, we immediately confirmed the lizard's body temperature with a quick-reading cloacal thermometer.

A different subset of hatchlings was used to test climbing speed using the protocol above. Climbing speed was measured on a 1-m electronic racetrack with photocells placed every 25 cm, and tilted to an angle of 80° . Wire screen (5 mm mesh width) was used as a substrate to mimic climbing conditions up bark and in a vegetation matrix. The raceway measured 6.5 cm wide during the 2007 trials. We increased the width of the raceway to 9.5 cm and also affixed wire screen to both raceway walls in 2008 after post-evaluating climb video files (used for documentation purposes) and noting that iguanas attempted to use the side walls while climbing. Consequently, faster speeds in 2008 were most likely the result of the wider raceway and wire mesh affixed to the side walls (see Results).

Telemetry Study

We affixed BD-2 (0.78 or 0.85 g; $14 \times 6.5 \times 3.5$ mm) and BD-2N (0.62 g; $13 \times 6.5 \times 2.8$ mm) transmitters to the dorsal inguinal region of a different subset of hatchlings using Torbot bonding cement (Torbot Group Inc., Cranston, RI). In July 2007, we tracked two iguana groups representing 5.0% and 7.5% transmitter to BM ratios. In July 2008, we tracked two iguana groups representing 5.0% and 10.0% transmitter to BM ratios. In 2007, we observed telemetered iguanas grouping with free-ranging hatchlings in the area. Consequently, we released a control group in 2008 with no external transmitters. We standardized transmitter to BM ratios using 20-gauge utility wire threaded through an anterior tube embedded in the transmitter and then coiled around the transmitter in a horizontal spiral. For visual identification at a distance, we marked hatchlings externally with

painted numbers on each side of the body using white correction fluid. Although we did not evaluate the effect of painted numbers on the lateral sides of iguanas, all hatchlings were painted similarly and thus any potential effects were equalized among individuals. We placed hatchlings in a cardboard box located at the beach/forest transition zone in the Gandoca-Manzanillo Wildlife Refuge and allowed them to leave on their own.

We tracked iguana hatchlings using a handheld 3-element Yagi directional antenna and a Wildlife Materials, Inc. (Carbondale, IL, USA) TRX-48S receiver. Telemetered iguanas were located daily during the day and evening. We searched systematically for control iguanas daily in and between areas occupied by telemetered iguanas. After locating an iguana, we recorded time, straight-line distance from release site, and location using a WAAS-enabled Garmin® 76CSx GPS receiver. We confirmed iguana locations by visual observation when possible to ensure that we were recording actual hatchling movement patterns and not predators with ingested transmitters. We tracked iguanas up to 24 and 30 days in 2007 and 2008, respectively. At the end of the study, we captured hatchlings at night, removed their transmitters, and recorded SVL, BM, and noted instances of tail autotomy.

Statistical Analyses

We tested for transmitter-burdening effects on sprint and climb speeds using repeated-measures ANOVA on performance speeds with transmitter-to-body-mass ratio as the within-subjects factor. The data were analyzed both with and without snout-vent length (SVL) as a covariate. Results did not differ between these methods, so only analyses without covariates are reported. Although potential problems using ratios in statistics have been noted (Packard and Boardman, 1999), the context in which ratios were applied in our study differs from traditional morphological or physiological studies. In our study, we used fixed ratios to create independent categories of transmitter burdening levels. We manipulated only the numerator (transmitter mass) with a constant denominator (BM) for each animal in a repeated measures design. Moreover, there were no

correlations between BM, and climb and sprint speeds for control groups over the three measured variables (initial, maximum burst, and overall speed). Prior to analyses, all data were tested for normality, homogeneity of variances, and sphericity. Data not conforming to these tests were log transformed. Because the assumption of sphericity required for repeated measures was not met for the 2008 maximum sprint speed (Huynh-Feldt $\epsilon = 0.88$), the degrees of freedom for the analysis were corrected using the Huynh-Feldt estimates of sphericity. Significant effects for all repeated-measures tests were investigated further using Tukey's post-hoc multiple-comparison tests. Differences in morphometrics, straight-line distance from release site, and percent growth between treatment groups were compared using Student *t*-tests and one-way ANOVA with post-hoc multiple comparisons. Corresponding non-parametric Kruskal-Wallis tests were used when sample sizes fell below 10 for any treatment group. Non-parametric post-hoc multiple comparisons were made using sequential Mann-Whitney *U* tests with Bonferroni adjustments for multiple comparisons.

Survival estimates of released hatchlings were calculated using the Kaplan-Meier procedure (Kaplan and Meier, 1958). Fates of hatchlings were documented as alive at the end of the study, dead by observed predator events, or as transmitters recovered (typically underground in crab burrows or on the ground). Most transmitters recovered without iguanas had signs of predator-inflicted damage (e.g., abrasions, damaged antennas). The log-rank test was used to compare survival-distribution functions between treatments for each year and for treatments among years. Survival estimates for control iguanas in 2008 are conservative because iguanas were not tracked actively using telemetry. Thus, the day that control iguanas remained undetected for the duration of the study was the date recorded as a death event. These data were most likely not indicative of true survival patterns because control iguanas may have migrated away from the primary study areas or eluded detection. Nevertheless, the calculation provides a baseline survival estimate.

TABLE 1.—Mean sprint and climb speeds with ± 1 SD for green iguana hatchlings affixed with external transmitters. Statistical tests with significance levels are included. Significant results are in bold.

	Initial speed (cm s ⁻¹)	Maximum speed (cm s ⁻¹)	Overall speed (cm s ⁻¹)
Sprint 2007 (n = 22)			
Control	108.63 \pm 33.73	223.03 \pm 34.19	125.51 \pm 19.52
2.5%	106.06 \pm 26.21	218.43 \pm 36.38	116.00 \pm 17.97
5.0%	114.07 \pm 31.76	224.41 \pm 35.50	120.93 \pm 19.89
7.5%	105.93 \pm 28.86	221.74 \pm 43.38	115.01 \pm 16.97
Repeated-measures ANOVA	$F_{3,63} = 0.370, P = 0.77$	$F_{3,63} = 0.105, P = 0.96$	$F_{3,63} = 2.505, P = 0.07$
Climb 2007 (n = 22)			
Control	35.17 \pm 6.16	99.81 \pm 25.59	28.07 \pm 8.20
2.5%	33.52 \pm 7.15	95.16 \pm 25.64	28.07 \pm 8.95
5.0%	32.36 \pm 5.57	87.96 \pm 24.53	26.01 \pm 6.62
7.5%	32.40 \pm 5.57	82.93 \pm 21.70	25.15 \pm 7.26
Repeated-measures ANOVA	$F_{3,63} = 2.203, P = 0.09$	$F_{3,63} = 2.532, P = 0.07$	$F_{3,63} = 1.508, P = 0.22$
Sprint 2008 (n = 22)			
Control	123.34 \pm 16.59	218.18 \pm 16.81	150.21 \pm 18.80
5.0%	123.86 \pm 20.37	215.52 \pm 19.74	148.22 \pm 19.26
10.0%	120.94 \pm 17.70	207.96 \pm 14.12	142.84 \pm 14.47
15.0%	118.31 \pm 12.45	210.80 \pm 16.36	142.75 \pm 15.05
Repeated-measures ANOVA	$F_{3,63} = 0.543, P = 0.66$	$F_{2,6,55.5} = 2.326, P = 0.06$	$F_{3,63} = 2.579, P = 0.06$
Climb 2008 (n = 27)			
Control	42.81 \pm 7.66 a	106.98 \pm 13.75 a	53.05 \pm 6.37 a
5.0%	42.10 \pm 8.48 ab	105.73 \pm 15.88 a	52.08 \pm 6.82 ab
10.0%	40.65 \pm 8.47 ab	86.64 \pm 13.81 b	49.03 \pm 6.44 b
15.0%	38.93 \pm 6.71 b	85.89 \pm 14.14 b	47.83 \pm 7.20 b
Repeated-measures ANOVA	$F_{3,78} = 3.675, \mathbf{P = 0.02}$	$F_{3,78} = 25.553, \mathbf{P \le 0.01}$	$F_{3,78} = 6.212, \mathbf{P \le 0.01}$

RESULTS

Transmitter burdening affected sprint and climbing speeds differently (summarized in Table 1). Sprint speeds for all performance variables (initial, maximum, overall) in both years (2007 and 2008) did not differ between any treatment group (all $F \leq 2.579$, all $P \geq 0.06$; Table 1). Climb speeds for all performance variables in 2007 also did not differ between controls and treatment groups (all $F \leq 2.532$, all $P \geq 0.07$; Table 1). Climb speeds for all performance variables in 2008, however, did differ statistically (Table 1). Initial climb speed was faster for the control group than for the 15.0% treatment group (mean difference = 3.88 cm s⁻¹, $P < 0.01$, $\omega^2 = 0.60$). Maximum climb speed differed between the two lower (control, 5.0%) and the two higher (10.0%, 15.0%) treatment groups with a mean difference of 20.09 cm s⁻¹ ($P < 0.01$; control versus 10.0% $\omega^2 = 0.76$; control versus 15.0% $\omega^2 = 0.73$). Overall climb speed differed between the control and two higher (10.0%, 15.0%) treatment groups, with a mean

difference of 4.62 cm s⁻¹ ($P < 0.01$; control versus 10.0% $\omega^2 = 0.51$; control versus 15.0% $\omega^2 = 0.58$).

The initial body size for iguanas recaptured at the end of the 2007 telemetry study differed between the 5.0 and 7.5% treatment groups (SVL: $t_{24} = 2.129, P = 0.04$; BM: $t_{24} = 4.682, P < 0.01$). These body-size differences remained statistically significant at the end of the 24 day study period ($t_{24} \geq 2.040$, all $P \leq 0.05$; Table 2). The percentage increases in SVL and BM at the end of the study for both treatment groups, however, did not differ statistically ($t_{24} \leq 0.402$, all $P \geq 0.69$; Table 2).

The initial body size for iguanas recaptured at the end of the 2008 telemetry study did not differ between the control and treatment groups (SVL: Kruskal-Wallis $H = 2.362, P = 0.31$; BM: Kruskal-Wallis $H = 1.865, P = 0.39$). Body sizes for recaptured iguanas remained statistically similar at the end of the 30 day study period (SVL: Kruskal-Wallis $H = 0.910, P = 0.64$; BM: Kruskal-Wallis $H = 3.882, P = 0.14$; Table 2). Though the

TABLE 2.—Mean body sizes, percentage growth, and distance from release site for green iguana hatchlings released and radio tracked in the Gandoca-Manzanillo Wildlife Refuge, Costa Rica. Means are presented with ± 1 SD. Statistical tests (student *t*-tests in 2007; one-way ANOVA and Kruskal–Wallis in 2008) with significance levels are included. Significant results are in bold.

Year	Group	Pre-release SVL (cm)	Pre-release BM (g)	Recapture SVL (cm)	Recapture BM (g)	% SVL increase	% BM increase	Distance from release (m)
2007	5.0%	7.83 \pm 0.27 (n = 23)	16.63 \pm 1.44 (n = 23)	8.17 \pm 0.28 (n = 15)	19.99 \pm 2.88 (n = 15)	4.86 \pm 3.61 (n = 15)	19.13 \pm 13.64 (n = 15)	140.00 \pm 63.12 (n = 15)
	7.5%	7.63 \pm 0.08 (n = 19)	14.41 \pm 0.99 (n = 19)	7.97 \pm 0.06 (n = 11)	16.47 \pm 2.53 (n = 11)	4.90 \pm 3.13 (n = 11)	16.48 \pm 19.30 (n = 11)	124.09 \pm 43.82 (n = 11)
		$t_{40} = 2.592$ P = 0.01	$t_{40} = 5.710$ P = 0.00	$t_{24} = 2.040$ P = 0.05	$t_{24} = 3.229$ P = 0.01	$t_{24} = -0.031$ P = 0.98	$t_{24} = 0.402$ P = 0.69	$t_{24} = 0.717$ P = 0.48
	control	7.46 \pm 0.35 (n = 23)	12.59 \pm 2.14 (n = 23)	7.81 \pm 0.16 (n = 8)	17.91 \pm 1.75 (n = 8)	7.15 \pm 3.40 (n = 8)	46.50 \pm 19.85 (n = 8)	141.13 \pm 33.11 (n = 8)
2008	5.0%	7.64 \pm 0.43 (n = 24)	14.11 \pm 2.14 (n = 24)	7.90 \pm 0.47 (n = 10)	17.47 \pm 3.43 (n = 10)	5.12 \pm 3.84 (n = 10)	31.45 \pm 5.83 (n = 10)	146.20 \pm 35.21 (n = 15)
	10.0%	7.41 \pm 0.46 (n = 25)	12.49 \pm 2.13 (n = 25)	7.82 \pm 0.51 (n = 10)	15.26 \pm 2.80 (n = 10)	5.59 \pm 2.35 (n = 10)	24.98 \pm 7.62 (n = 10)	141.75 \pm 39.45 (n = 12)
		$F_{2,69} = 2.081$ P = 0.13	$F_{2,69} = 4.392$ P = 0.02	$H = 0.910$ P = 0.64	$H = 3.882$ P = 0.14	$H = 2.135$ P = 0.34	$H = 7.071$ P = 0.03	$H = 0.234$ P = 0.89

percentage increase in SVL at the end of the study did not differ between control and treatment groups (Kruskal–Wallis $H = 2.135$, $P = 0.34$; Table 2), the percentage increase in BM did differ between control and treatment groups (Kruskal–Wallis $H = 7.071$, $P = 0.03$; Table 2). Post-hoc tests with Bonferroni adjustments revealed a marginally significant difference between the control and 10.0% treatment groups (Mann–Whitney $U = 14.0$, $P = 0.02$). The percentage increase in BM at the end of the study for the 10.0% treatment group averaged 21.5% less than for the control group (Table 2).

The probability of survival did not differ between the 5.0% and 7.5% treatment groups in 2007 (log-rank test $\chi^2 = 0.05$, $P = 0.82$) or the 5.0% and 10.0% treatment groups in 2008 (log-rank test $\chi^2 = 0.11$, $P = 0.74$). In fact, excluding the control group, the probability of survival did not differ statistically between any treatment groups over both years (log-rank test $\chi^3 = 2.61$, $P = 0.46$). The probability of survival for the 5.0% and 7.5% treatment groups in 2007 was 65.2% (mean survival time = 20 d; 95% CI = 16–23 d) and 57.9% (mean survival time = 19 d; 95% CI = 16–21 d), respectively (Fig. 1A). The probability of survival for the control, 5.0%, and 10.0% treatment groups in 2008 was 34.8% (mean survival time = 11 d; 95% CI = 5–16 d), 57.7% (mean survival time = 19 d; 95% CI = 14–24 d), and 52.2% (mean survival time = 17 d; 95% CI = 12–22 d), respectively (Fig. 1B). Finally, the mean straight-line distance from the release sight at the end of both study periods (2007 and 2008) did not differ between treatment groups ($P \geq 0.48$; Table 2).

DISCUSSION

In this study, transmitter burdening had variable effects on locomotor performance and percentage BM growth, but not on survival. Our laboratory trials indicated that sprint speeds were not reduced significantly with transmitters of up to 15.0% body mass (Table 1). In other studies, adult gravid green iguanas have demonstrated the ability to match the acceleration of non-gravid females, despite reproductive loads between 31–63% of maternal mass (Scales and

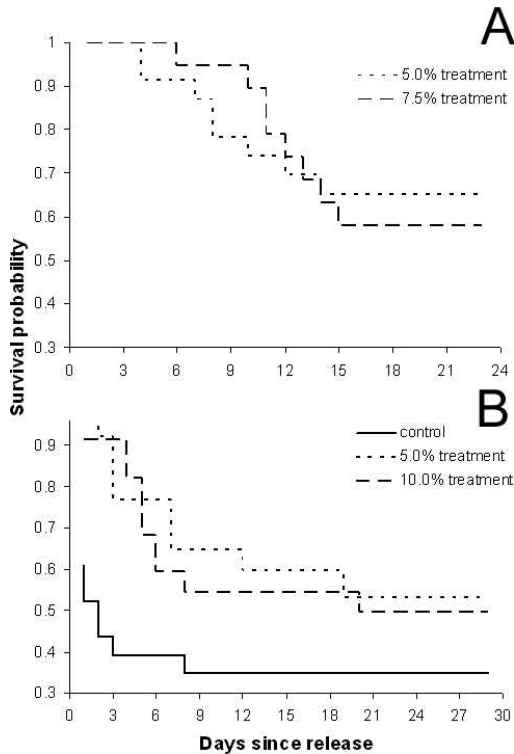


FIG. 1.—Kaplan–Meier survival curves for green iguana hatchlings released in the Gandoca-Manzanillo Wildlife Refuge, Costa Rica. (A) Iguanas released in 2007 included two treatment groups, with the dotted line representing the 5.0% and hatched line representing the 7.5% treatment group, respectively. (B) Iguanas released in 2008 included three treatment groups, with the solid line representing the control group, the dotted line representing the 5.0%, and the hatched line representing the 10.0% treatment group, respectively. Survival estimates for control iguanas are conservative (see Materials and Methods).

Butler, 2007). In an effort to isolate potential physiological modifications associated with the gravid state, Shine (2003) demonstrated a non-appreciable reduction in running speeds of up to 20% the body mass of fluid-injected skinks. These results support our data that transmitter burdening of up to 15.0% body mass has a non-appreciable effect on sprint speed for hatchling green iguanas in the laboratory.

Climb speeds were reduced across two of three performance variables at the 10% burdening level (Table 1), suggesting that 7.5% transmitter to BM ratio is a performance threshold for climbing performance. Van

Marken Lichtenbelt et al. (1993) demonstrated that climbing was approximately six times more costly energetically than movement on a horizontal surface for green iguanas. These data are consistent with other laboratory studies in lizards that illustrate movement up steep inclines is more expensive energetically (Farley and Emshwiller, 1996). Thus, the energetic cost associated with climbing activity may explain the reduced performance observed in our study.

For telemetered iguanas, percentage BM growth was significantly less for iguanas affixed with 10.0% transmitters than for control iguanas. This result suggests that carrying a heavier transmitter relative to BM can incur more energetic costs, especially since our iguanas made extensive vertical movements daily from lower positions to higher positions at night (C. Knapp and J. Abarca, unpublished data). The higher energetic costs associated with transporting heavier transmitters could reduce energy that would otherwise be allocated to growth or energy reserves. These reductions over an extended period can potentially lower fitness by reducing clutch sizes or delaying maturity (Osborne et al., 1997; Weatherhead and Blouin-Demers, 2004).

We found no differences in survival probabilities between telemetered treatment groups. Ideally for comparison, we would have a more conclusive data set for survival using our control group, but the extreme cryptic nature of hatchlings and the ability to disperse unimpeded through the study site made finding all non-telemetered hatchlings unrealistic. However, the power of this survival study is that the control animals provided a baseline estimate of survival in a native tropical environment with an abundant suite of predators. Whether or not the survival of non-telemetered control iguanas was appreciably higher than telemetered iguanas is unknown. Indeed, survival of non-telemetered green iguana hatchlings observed (not inferred from future recaptures) over a 68 day period in Colombia was estimated at 16.2% (Table 9.1 in Harris, 1982). Therefore, our estimate of 34.8% for non-telemetered controls over a 30 day period either reveals additional mortality between 30 and 68 days

or underscores the benefits of telemetry in estimating survival of free-ranging lizards. Telemetry studies over extended periods are needed to investigate this potential discrepancy further.

The cryptic and secretive nature of green iguana hatchlings (Henderson, 1974) may influence their susceptibility to different predators, thereby reducing the biological significance of any decrements in locomotor performance caused by transmitters. Predators often rely on different foraging strategies (Perry, 1999), and in some cases the vulnerability of iguana hatchlings in our study site may have been influenced more by the predator's probability of detecting an iguana than by its probability of capturing an iguana after detection (Schwarzkopf and Shine, 1992). For example, we observed a control hatchling being eaten by a brown vine snake (*Oxybelis aeneus*) while a telemetered hatchling was less than one meter away in the same shrub. We also recaptured a telemetered iguana in the 10.0% treatment group with a truncated tail, suggesting that it was successful in escaping predation by using caudal autotomy (Arnold, 1988). Most likely, however, a combination of crypsis, physiological state, and associated locomotor performance plays a role in survival for green iguana hatchlings (Christian and Tracy, 1981), as our hatchlings fled rapidly along the ground while leaving the release site (as in Greene et al., 1978) and were susceptible to attacks from crabs and birds.

Study Considerations

Attachment techniques for external transmitters can generally affect survival (Gervais et al., 2006), suggesting that the physical constraints imposed by an external transmitter should be considered seriously. Future projects should focus on investigating the effects of mass burdening versus physical burdening by studying the survival of lizards with internally implanted versus externally affixed transmitters. Attachment methodology should also be evaluated continuously and problems reported to peers and wildlife managers. The glue technique used in this study caused minor burns in the area of attachment for some iguanas. These burns appeared to have no long-term effect to iguanas kept in cages

for monitoring. Inevitably, as attachment techniques expand, so will unanticipated consequences. Indeed, while studying the Jacky dragon (*Amphibolurus muricatus*), Warner et al. (2006) noted that in limited cases, telemetry units or harness mechanisms became entangled in vegetation. Knapp and Owens (2005b) reported using attachment techniques that caused minor lacerations in the inguinal region for rock iguana hatchlings (*Cyclura cychlura*). Telemetered lizards should therefore be monitored as frequently as possible, without disturbing individuals, in order to detect problems associated with attachment techniques or animal stress.

New transmitters are now available with greatly reduced mass (0.2 g) and volume (Naef-Daenzer et al., 2005), which will allow telemetry applications to be expanded to smaller lizards. The potential ecological applications, especially for secretive species, are exciting but future assessment studies must be expanded to include lizard taxa encompassing a diverse range of body sizes and life histories. For example, lizards in general often differ in foraging behavior, with some lizards relying on infrequent, fast movements for capturing prey while others move actively and frequently (Perry, 1999). Foraging lizards can therefore vary substantially in metabolic rates across species (Nagy et al., 1984), and thus daily energetic expenditures should be considered before initiating telemetry studies for any species. Species may also use different escape tactics (e.g., jumping versus sprinting), thus making general assessments of transmitter impacts difficult over multiple taxa. Therefore, researchers must be proactive in evaluating the energetic expenditures, foraging strategy, and escape responses of focal species to minimize effects of transmitter and attachment techniques.

Multiple factors of a species biology including morphology, energetic constraints, and habitat use will affect its sensitivity to the external attachment of a transmitter. It is therefore difficult to draw general conclusions on maximum acceptable loads or attachment techniques since radio tagging probably affects species differently (Steenhof et al., 2006). However, realizing that interspecific-movement kinetics can influence locomotor

performance (Clemente et al., 2004), we can make inferences concerning the possible performance effects of transmitter burdening on similarly-sized lizards. For example, the rates of speed for sprinting and climbing in our study (Table 1) fall within published ranges of similarly-sized lizards (Vanhooydonck and Van Damme, 2001; Van Damme and Vanhooydonck, 2001) suggesting that our results may be applicable to other species. We suggest as a general rule that transmitter to body mass ratios for arboreal lizard species (or species with similar locomotor requirements) not exceed 7.5% based on lower climb performance in the laboratory for iguanas with $\geq 10.0\%$ transmitter packages. Additionally, though there were no differences in survival between treatment groups, our data suggest a lower relative mass gain for iguanas affixed with 10.0% transmitter to BM ratios. The extra energetic costs associated with carrying such a load may have fitness implications and should be avoided. In general, minimizing the impact on study animals, especially when working with imperiled species, should be a priority in order to avoid jeopardizing the health of study subjects.

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