Natural History of Neonatal Green Anacondas (*Eunectes murinus*): A Chip Off the Old Block

Jesús A. Rivas[1], Cesar R. Molina[2], Sarah J. Corey[1], and G. M. Burghardt[3]

Our knowledge of the biology of neonatal snakes has lagged behind that of adult animals, mostly due to the difficulty of finding and studying neonatal snakes in the wild. Traditional approaches view neonatal reptiles as miniature replicates of their adult counterparts. In this contribution, we present data on the natural history of neonatal Green Anacondas from opportunistic captures in the wild over a 17-year period, as well as from a brief study on captive-born radio-tagged individuals. Both approaches converge in presenting a picture of the ecology of neonatal anacondas showing many similarities between their natural history and that of adult anacondas in spite of the great size difference. The neonates' biology resembles that of adults, especially males, in their preference for birds in their diet, the relative prey size they choose, slow growth rates they experience, low feeding frequency, little mobility, and preference for similar habitats of stagnant, shallow water covered by aquatic vegetation. The conventional wisdom that neonatal reptiles are replicates of their adult counterparts seems to be largely on target in Green Anacondas.

Nuestro conocimiento sobre la biología de serpientes neonatales se ha quedado atrás en comparación con el conocimiento de serpientes adultas, mayormente debido a la dificultad de encontrar y estudiar serpientes recién nacidas en el campo. El entendimiento tradicional sobre la biología de reptiles reza que los neonatos son replicas en miniatura de los adultos. En esta contribución presentamos datos producto del estudio oportunista a largo plazo de la biohistoria de anacondas recién nacidas así como los resultados de un estudio breve de telemetría de anacondas neonatales nacidas en cautiverio. Ambos métodos convergen en presentar un cuadro de la biohistoria de anacondas neonatales consistente que muestra similitudes entre su biohistoria con la de anacondas adultas. La biología de los neonatos asemeja a las adultas en el tipo de presas que prefieren, tamaño relativo de las presas que consumen, una lenta tasa de crecimiento, poca movilidad y preferencia por hábitats con agua estancada, poco profunda y cubierta con vegetación acuática. La sabiduría convencional sobre biología de reptiles neonatos que propone que estos son réplicas en miniatura de los adultos, parece dar en el clavo con las anacondas verdes.

REPTILIAN life history studies have advanced largely based on comprehensive field and laboratory studies. However, understanding the biology of most reptiles has been challenged by the difficulty of acquiring field data from neonates due to their small size and secretive behavior (Dunham et al., 1994; Morafka, 1994; Morafka et al., 2000; Pike et al., 2008; Willson et al., 2008; Pizzatto et al., 2009). However, here we present some of the available studies on the biology and behavior of neonatal, hatchling, and juvenile reptiles beyond issues related to parental investment and incubation conditions. For example, there are several studies on social behavior of hatchling iguanas (Burghardt, 1977; Burghardt et al., 1977; Greene et al., 1978; Werner et al., 1987; Rivas and Levin, 2002), dispersal and orientation of neonatal turtles (Congdon et al., 2015; Ibañez and Vogt, 2015; Putman and Mansfield, 2015), and the field ecology of neonatal crocodilians (White and Rivas, 2003; Balaguera-Reina et al., 2015). The paucity of data is particularly noteworthy with snakes, where data from field studies are particularly lacking. There have been some studies on antipredator behavior (Herzog and Burghardt, 1986; Placyk and Burghardt, 2005; Gregory et al., 2007; Mori and Burghardt, 2008), snakes' innate dietary preferences (Burghardt, 1992; Burghardt and Krause, 1999; Burghardt et al., 2000), their ontogenetic switches (Mushinsky and Lotz, 1980; Savitzky and Burghardt, 2000), the ontogenetic changes in vipers' venom (Mackessy et al., 2003; Wray et al., 2015), and neonatal social behavior (Burghardt, 1983; Greene et al., 2002; Holycross and Fawcett, 2002; Cobb et al.,

2005; Jellen and Kowalski, 2007; Reiserer et al., 2008; Howze et al., 2012). Only one field study seems to have addressed the natural history of neonatal basal snakes (Pizzatto et al., 2009).

As noted, a major reason for the paucity of data on neonatal snakes is that their small size makes them difficult to find and observe. Even with the latest technology, most neonates are too small to equip with radio transmitters fitted with long-lasting batteries and survival may be low. However, there are exceptions, such as Green Anacondas, which due to their large size at birth are good candidates for studying neonatal behavior and ecology. At more than 220 g and 75 cm at birth (Rivas, 2000, 2008), neonatal anacondas are similar to, or larger than, adults of many other snake species and therefore can safely be fitted with radio transmitters.

Our understanding of the biology of adult Green Anacondas has improved in recent years. There have been comprehensive studies of their mating system (Rivas and Burghardt, 2001; Rivas et al., 2007a), general natural history (Rivas, 2000; Rivas et al., 2007b), conservation and sustainable use (Rivas, 2007, 2010), predation (Rivas et al., 1999, 2001; Rivas and Owens, 2000), diseases (Calle et al., 1994, 2001), foraging (Rivas, 1998, 2004), and demography (Rivas and Corey, 2008), along with notes on field techniques (Rivas et al., 1995; Raphael et al., 1996; Rivas, 2008). Adult anacondas live in shallow, stagnant water that is often covered by aquatic vegetation (Rivas, 2000; Rivas et al., 2007b). They are ambush hunters that may go for long periods without a meal, although when they do eat they can take quite large meals.

---

[1] New Mexico Highlands University, Department of Biology, 1005 Diamond Avenue, Las Vegas, New Mexico 87701; Email: (JAR) rivas@nmhu.edu; and (SJC) sjcorey@nmhu.edu. Send reprint requests to JAR.

[2] Universidad Central de Venezuela, Instituto de Zoología Tropical, Apartado 1041, Caracas, Venezuela. Deceased.

[3] Departments of Psychology and Ecology and Evolutionary Biology, University of Tennessee, Knoxville, Tennessee 37996; Email: gburghar@utk.edu.

Smaller anacondas prey mostly on birds. This is true for both juvenile females and most males throughout their lives, but as soon as females reach reproductive size, which is larger than the maximum size obtained by most males, they switch to feeding on mammals and reptiles (Rivas, 2000). Growth rates decline in adulthood; there is a documented case of an adult free-ranging anaconda taking 13 years to grow little more than half a meter (Rivas and Corey, 2008). Adult anacondas may be found in aggregations during the dry season where they apparently gather in cave-like depressions that are exposed in the river banks when the water level drops, or the few ponds that hold water until the wet season returns. During this time the snakes are essentially stationary and appear tolerant to close proximity of conspecifics (Rivas, 2000).

The view that neonatal reptiles are miniature replicas of adults and undergo few ontogenetic behavioral changes outside of reproduction that are not mere consequences of changes in body size has been challenged by evidence of significant ontogenetic changes in diet (Mushinsky and Lotz, 1980) and other behavioral changes associated with learning in early stages of development (Gove and Burghardt, 1975; Burghardt and Krause, 1999; Burghardt et al., 2000; Waters and Burghardt, 2013). Neonatal animals are expected to have higher energetic requirements than adults (Nagy, 2000) and different metabolic requirements due to the scaling of metabolic processes (Calder, 1996). Thus, we should expect differences between the life history of neonates and adults of the same species, such as neonates having higher activity, foraging more often, and showing more mobility than adults.

Here we present data from opportunistic observations of neonatal wild-caught anacondas on diet, mobility, behavior, growth rate, and habitat use collected over a 17-year period, as well as from a brief radio-telemetry study done with captive-born neonatal anacondas. We compare the results of both approaches with what is known of adult anacondas from previous studies.

MATERIALS AND METHODS

Study animals.—An obvious initial problem we faced was accurately defining a neonate. In our long-term study of Green Anacondas, we found neonate-sized individuals several months after the parturition season. Newborn anacondas have umbilical scars, but these can still be found four months after birth in some individuals, while other individuals, of presumably the same age, did not show them. Because the birth season is from September to November (Rivas, 2000), all animals found at neonatal size in the March–April season are presumably between 3 to 7 months old. Since growth is strongly influenced by food intake, an older neonate-sized individual may face the same ecological challenges as a true neonate in terms of temperature regulation, predators, and prey availability. However, being older, it may have different cognitive and experiential abilities than a newborn animal. Not wanting to set an arbitrary limit, we graphed the cumulative frequency of anaconda sizes from 788 animals caught over 17 non-consecutive years. There was a generally continuous distribution of sizes except for a gap in the distribution in the early classes (Fig. 1). We believe that the break in the distribution corresponds to the most recent cohort of the population. We chose 92 cm as the cut off for defining a neonate, as it is near the midpoint between the largest of the neonate class (84.6
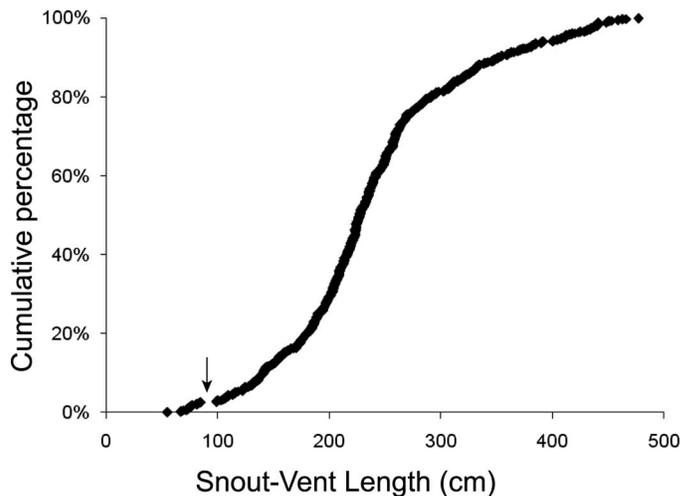
Fig. 1. Cumulative distribution of sizes of 788 Green Anacondas (*Eunectes murinus*) from a 17-year study in the Venezuelan llanos. We used the natural break in the distribution of the population for the cut off between neonates and the rest of the population (cut off, 91.75 cm, indicated by arrow).

cm) and the smallest of the larger class (98.9 cm). Larger animals are almost certainly older than one year of age.

Study site.—We have been studying the natural history of anacondas since 1992 in the Venezuelan llanos at Hato El Cedral, a 54,000 ha cattle ranch located in the Muñoz district (7°30′N and 69°18′W) of Apure State (Rivas, 2000). The sampling area was approximately 6 km^2 surrounding the station. During March and April, which comprise the driest part of the dry season, we looked for animals in the swamp and other aquatic habitats. The predominant vegetation associated with this hyper-seasonal savanna involves few trees, grasses, and shrubs that may be dense near water. A series of human-made dikes have created more permanently flooded habitats ("módulos") where the impact of the dry season is diminished. The gates of the dikes are closed at the end of the wet season to hold water for pastures and cattle. Construction of elevated roads required dirt taken from surrounding areas, which produced a series of artificial ponds or borrow pits. Although artificial in origin, the borrow pits resemble natural depressions that occur in the landscape. They often are covered by aquatic vegetation, mostly water hyacinths (*Eichhornia crassipes*, *E. azurea*) and an aquatic fern (*Salvinia* sp.). Borrow pits are used by different animals that either live in or near them, or that visit them to drink (for a complete description of the habitat, see Rivas et al., 2002).

Survival.—Despite their size, anacondas are anything but conspicuous. The dry season (in particular March through May) provides the best time for finding wild anacondas because all of the snakes that live in the flooded savanna gather in the few depressions that hold water. We systematically searched all the bodies of water in the study area with water depths less than 50 cm. Search parties were anywhere between two to six people wading through the vegetation looking for snakes by feeling under the water and probing with sticks (see Rivas et al., 2007b for a complete description of search and capture). During the first six years (1992–1997), we sampled for about six hours a day for 55 days per season. We were not able to collect data every year after 1997, and during the years we collected data (2002, 2003, 2007, 2009,

Table 1. Measurements and activity of neonate Green Anacondas implanted with radio transmitters. TL = total length, SVL = snout–vent length, TNL = total number of localizations, Time = number of days that the animal was under study, WD = water depth, PV = percentage of times the animal was visible, HR = home range is the surface area, in hectares, used by the animal calculated by the maximum convex polygon. ADM = average distance per move (in meters) and ADD = average daily distance moved per day. An asterisk (*) indicates snakes that were killed by predators during the study.

Name	TL	SVL	Mass	Sex	TNL	Time	WD	PV	HR	ADM	ADD
Cassie*	84.7	76.1	210	F	14	22	19.5	0	0.464	37.83	10.01
The Beast	79	67.5	200	M	10	22	17.5	33.3	0.013	6.42	2.47
Ingrid*	86	74.6	190	F	15	22	30	0	0.008	11.24	3.28
Pedro	83.7	72.8	180	M	13	17	11.33	0	0.008	4.08	2.4
Angelica	88.3	76.3	230	F	20	28	17.45	52.6	0.017	7.02	4.09
Average	84.3	73.5	202		14.4	19	19.16	17.2	0.102	13.32	4.45

and 2011), the sampling effort was limited to two weeks. In a parallel study of reproductive biology, we marked 278 captive-born anacondas in 1995 and 1996 and released them at the study site (where the mothers were collected) to assess neonatal survival in the wild.

Diet.—Some animals were found in the process of constricting prey or having recently eaten a meal. If the animal had recently eaten, we kept it in a burlap bag and waited until the snake defecated before it was returned to the place of capture. The feces were then preserved in 70% ethanol, and prey remains were identified in the lab or with a reference collection by specialists. Prey capture rate is low in wild anacondas (Rivas et al., 2007b). To avoid negatively affecting their growth and survival, we therefore refrained from removing prey from stomachs. We did not use the post-defecation mass for the snakes for calculations of "net snake mass" because we could not be sure that remnants of the prey were not increasing the mass of the snake. When we could not weigh birds, we obtained the mass reported in the literature (Hilty, 2003) since the mass of birds varies little after they fledge. With mammals or birds that we could not identify, we calculated the expected mass of the snake based on the following empirical regression: Log(mass) = 2.9565 × Log(svl)–3.0902 ($n = 770$; $R^2 = 0.95$) obtained for Green Anacondas in the same area (Rivas, unpubl. data). The prey mass was calculated as the difference of the recorded mass of the anaconda and prey minus the calculated mass for the anaconda. Relative prey size was calculated using the snake mass excluding the prey mass, so the prey mass was not used twice in the same calculation.

Habitat use.—Two pregnant female anacondas were collected in the dry season (April) 1995 and kept in captivity until they gave birth in November. Neonates from both clutches were mixed and maintained in enclosures until January, when five individuals were selected for implantation of radio transmitters. Table 1 shows the data from neonates used in the telemetry study. The neonates were not fed in captivity to prevent biasing of prey preferences in the naïve animals (Burghardt, 1992). Field observations indicate that this level of fasting is not uncommon among neonatal anacondas (Rivas, 2000; Rivas et al., 2007b). Transmitters (AVM, model SM1-H) were 37 mm long, 9.5 mm wide, 6 mm thick, and weighed 4 g with a 20 cm long antenna and a four-month expected life span. Transmitter-implanted neonates had an average mass of 202 g, so the transmitters represented about 2% of the neonatal mass. Transmitters were implanted in two male and two female neonates. Subcutaneous infiltration of 0.03% lidocaine was used for local anesthesia, and the

transmitters were implanted subcutaneously (Raphael et al., 1996).

We released the neonates, with their mothers, 24 h after implantation in the borrow pits closest to where the mothers had been caught in the wet season. We determined locations of the neonates by radio telemetry approximately every other day. We recorded data on their position, water depth, vegetation, habitat, and movements. Two of the individuals were killed by predators within a month (Rivas et al., 2001). The transmitter of one of these animals was then re-implanted in an animal from one of the same clutches (see Angelica on Table 1) that had been kept in captivity for such an eventuality. We plotted the locations on a map and used the 100% Maximum Convex Polygon method (White and Garrot, 1990) to estimate the home range of each animal using Arcmap (ESRI, 2006, ArcMap Version 9.2. Environmental Systems Research Institute, Redlands, CA).

RESULTS

Survival.—Of a sample of 696 wild-caught anacondas from the study area, only 25 (3.6%) were classified as neonates. Of these 25 animals, only two (8%) were recaptured in a later year. Of the 278 neonates released from pregnant females, none were caught in any later year, at any size. Of the 25 wild-caught neonates for which data were available, 23 were found in shallow, stagnant water under plant cover either in a borrow pit (13) or along the edges of a módulo (10) with only two found in a savanna creek. Eight (32%) wild neonates were moving on the road, five (20%) were foraging/catching prey, six (24%) were basking, three (12%) were found buried under the mud, and three (4%) were swimming on the surface in open water or under aquatic vegetation. The two recaptured, wild-caught neonates grew at rates of 0.068 and 0.074 mm/day, respectively, over an 11-month period. The one with the lower growth rate was missing an eye at the time of the first capture. Surprisingly, it was still alive the next year despite this apparent handicap.

The average prey size of neonatal anacondas was 26.3% of the snake's pre-meal mass. Eight of the 25 (32%) wild-caught neonates found were either consuming or had recently ingested a meal. Seven of the nine prey items obtained from neonates were birds and two were mammals (Table 2). We did not find any fish, reptile, or amphibian remains.

Habitat use.—Radio-tagged animals moved little (Table 1), resulting in a considerable overlap of individuals' home ranges (Fig. 2). About a month into the study, the transmitters failed as they stopped putting out a regular beep (three months ahead of schedule). We also noted that at this time the incision for the implantation had not closed in three out of five neonates.

Table 2. Neonate anacondas in the Venezuelan llanos found with evidence of a recent meal. We used the reported mass of the prey (Hilty, 2003) and subtracted it from the mass of snake and prey to calculate the snake net mass. When the prey mass was unknown, we estimated the mass of the prey by subtracting the estimated mass of the anaconda based on its SVL. These cases are indicated with an asterisk (*). RPS = relative prey size. In this table we also include a neonate that was born in a naturalistic enclosure and that caught a bird before it was found in the birth cage.

ID	SVL (cm)	Mass (g)	Prey item	Prey size (g)	RPS %
E247C	73	262.25*	Unknown mammal	112.75	42.99
E498C	81.5	336.19*	Unknown mammal	96.81	26.65
E1008C	58.03	180	*Jacana jacana*	40	22.22
E1009C	82	335	*Crotophaga ani*	101.55	30.31
E1012C	75.43	440	*Jacana jacana*	80	18.18
E738	73.8	315	*Crotophaga ani*	100	31.75
E861C	76.5	301.19*	Passerinae	51.18	16.31
E588	81.8	460	*Jacana jacana*	70	15.22
Captive	73	195	*Phacellodomus rufifrons*	21.5	11.03

Telemetered neonates were always found in shallow water and rarely in water deeper than 20 cm. They were concealed by their cryptic coloration and coiled within the bulbs and roots of *E. crassipes* (73%), in a combination of *E. crassipes* and *Salvinia* sp. (20%), in grasses with *Salvinia* sp. (3%), in *Salvinia* sp. only (3%), or in open water (1%). When located, the snakes often had their heads above the surface, facing the shore. All but one of the locations (98.6%) were in the same borrow pit where the snakes had been released; the remaining one was in a nearby creek.

The only instance in which an individual was found in any place other than a borrow pit was Cassie, a neonate observed
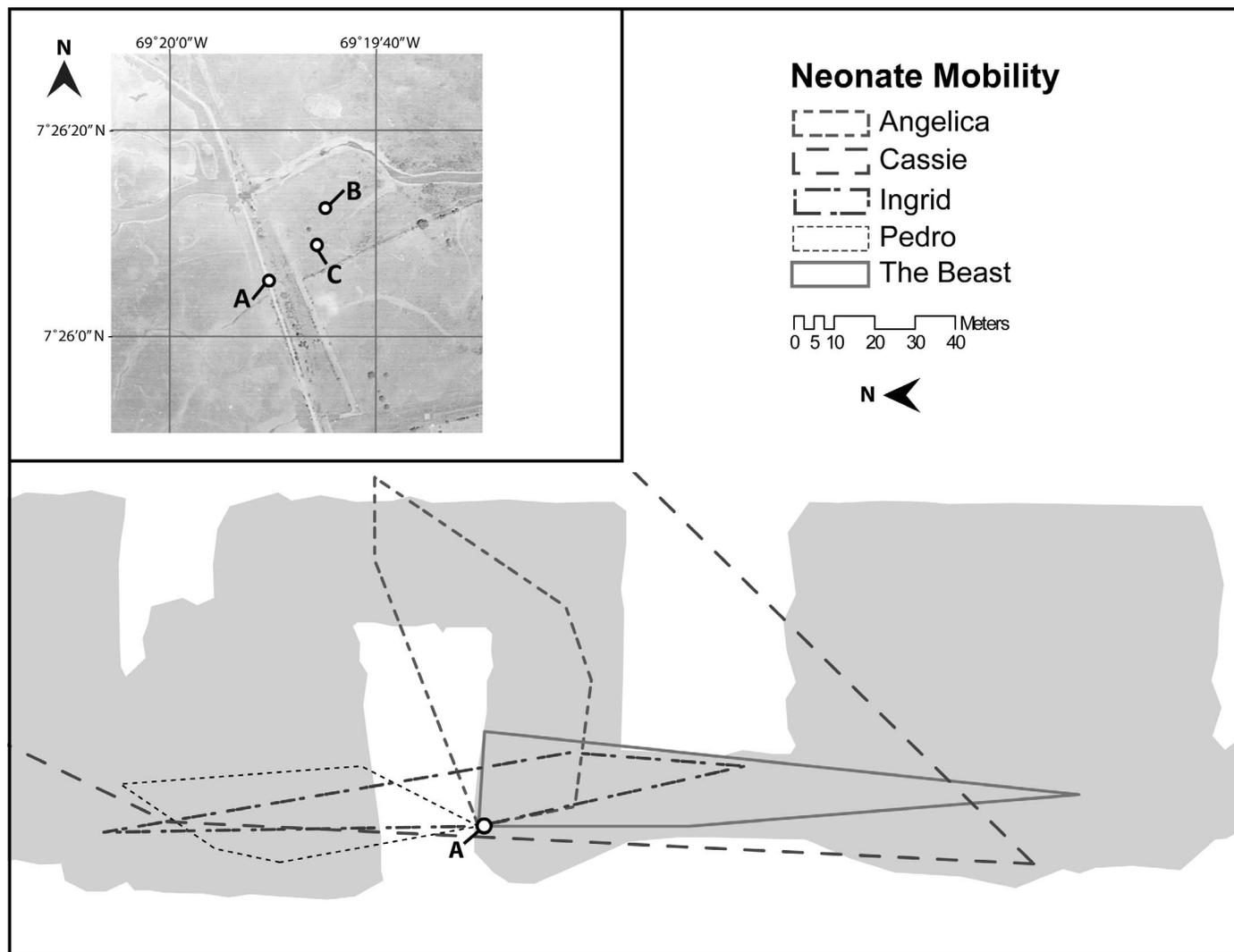
Fig. 2. Home ranges of radio-tagged neonatal Green Anacondas in the Hato El Cedral (Apure State, Venezuela), with water boundaries outlined in gray. Point A indicates where the neonates were released. Aerial map inset: Point A release location, B the last place where Cassie was seen alive, and C the place where the radio of Ingrid was found, presumably after a predation event. To the west was a módulo that held a large area of permanent water and to the north was a flowing river.

in a small creek that connects the borrow pits with a main river, 224 m northeast of the location where she was released. The next time this snake's radio signal was followed, Cassie's transmitter was found chewed up at the base of a tree that held a Crested Caracara (*Polyborus plancus*) nest (Rivas et al., 2001). Cassie was also one of the neonates that had moved most frequently (Fig. 2; Table 1). The other individual that showed more mobility, Ingrid, was also a victim of predation, which we documented by finding the transmitter in a bush away from the water with a chewed-up antenna (Rivas et al., 2001).

On day 10 after release, one of the neonates (see Pedro on Table 1) was observed with evidence of a recent meal. Of the five animals followed for approximately one month each, only Pedro showed evidence of having eaten. Although other habitats were available, neonates remained in a set of connected borrow pits heavily covered by water hyacinth at a mean water depth of 17 cm. Fifteen meters to the west, a large body of water confined by the road (labeled módulo in Fig. 2) had much deeper water, and approximately 50 m to the north was a permanent river. While the route to the módulo involved travel on dry land and consequent exposure to predators, the route to the river was through other borrow pits that had very similar habitats to the ones the neonates were utilizing, yet most neonates did not use it (Fig. 2).

DISCUSSION

Survival.—The neonate recapture rate of 8% was very low in comparison with the 24.7% found in adult anacondas (Rivas, unpubl. data). This difference could be due to at least two non-mutually exclusive reasons. First, neonates suffer higher mortality than adults, and second, neonates are more difficult to find due to their small size and crypsis. Since we rely on feeling them under the vegetation, the bodies of smaller animals would be less likely to be detected. We believe that low detection in neonates is a major reason for the low recapture rate. However, given that we have surveyed this population between 1992 and 2011, it would be remarkable if the paucity of recaptures was due to crypsis alone. We would presumably have recaptured the marked neonates as larger individuals in later years. Rather, the lack of recaptures suggests that juvenile mortality is high. Although recent simulation models suggest that neonatal mortality in reptiles is not as high as formerly believed (Pike et al., 2008), our data indicate that high neonatal mortality is likely the case in anacondas. That two out of five radio-tagged animals were preyed upon during the first month of life strongly supports this assumption (Rivas et al., 2001).

Growth rate.—The growth rate found among neonates appears low for animals that are expected to be in their peak growing period. This growth rate is also low when compared to the growth rate of captive neonatal anacondas fed regularly. We estimated growth rate from three neonates raised at the San Diego Zoo using their mass when they were acquired to estimate their length (length data were not available). Growth in the first 504 days is estimated to be 0.14 mm/day, twice that found in wild animals. Reported growth rate from other captive anacondas shows a neonatal growth rate as high as 2.13 mm/day in the first 445 days (Lamonica et al., 2007). The difference between the growth rate of captive animals is unclear. Likely it is due to different feeding regimes. What is certain is that neonatal anacondas have the capacity to grow much faster than they do in the wild.

The slow growth of wild animals may be due to limited food consumption. Even when wild animals have plenty of natural prey available, foraging may result in high exposure to predators. It is likely that the food intake of neonates is limited to the potential prey that moves within reach of the neonate in their retreats where the neonates both avoid predation and stalk prey. In fact, both of the recaptured animals mentioned above were re-caught the following year in exactly the same place they were found the first time, consistent with the notion of low mobility. This strategy might work well in the hyperseasonal savanna: neonates that venture out of the safe aquatic refugia during the pronounced dry season will be exposed to predators; on the other hand, staying in a shrinking body of water would be beneficial because it increases encounters with small birds (prey) that come to drink. Unfortunately no comparable study addresses other neonatal Boidae, so we lack a frame of reference to compare the growth rate of neonatal anacondas with snakes of comparable size. Perhaps the only baseline information that are comparable to anacondas in their ecology and phylogenetic position are aquatic pythons (*Liasis fuscus*). They are tropical constrictors that inhabit aquatic environments; however, with a body mass between 16 and 35 g at birth (Pizzatto et al., 2009), they are a fraction of the size of neonatal anacondas. In a long-term study on their ecology, Madsen and Shine (2000) found growth rates between 1 and 1.9 mm/day, far higher than that found in neonatal anacondas. Adult anacondas do have a very slow growth rate, even slower than that of neonates (Rivas and Corey, 2008).

Diet and prey size.—The diet of neonatal anacondas seems to be comprised mostly of birds, which is consistent with the diet of small adult anacondas (Rivas, 2000). Although we did not find evidence for predation by neonatal anacondas on hatchling spectacled caimans (*Caiman crocodilus*) or savanna sideneck turtles (*Podocnemis vogli*), these animals occupy the same habitat and are small enough to be potential prey. We were surprised at the absence of fishes and amphibians in the diets of neonatal anacondas, particularly in light of their abundance in shared habitats. Amphibians do not have keratinous structures that resist digestion and thus we would not have found them in feces. So, the lack of amphibian remnants does not necessarily indicate that neonatal anacondas avoid them. On the other hand, we would have found scales or some remnants of fishes if they were present in the diet. Our methods of sampling had another limitation: small prey items that did not make a noticeable lump would have gone unnoticed and we would not have obtained such feces for analysis. Amphibians and fishes are also missing in the diet of adult anacondas (Rivas, 2000).

The proportion of neonates that were found in the act of obtaining a meal seems high compared with that of adult anacondas (Fig. 3). This may be related to the need of young animals to gather energy to fuel growth. Nagy (2000) predicted that neonates would have higher metabolic activity and spend more time foraging and less time engaged in other activities such as thermoregulation and socialization. However, the activity pattern found in neonates might not accurately reflect the actual activity pattern of neonatal anacondas. Rather, certain activities make them more vulnerable to detection by both scientists and potential predators. In fact, 71% of the observations were from animals
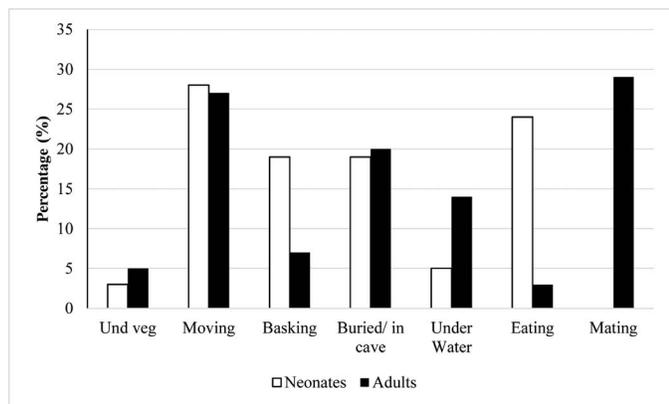
Fig. 3. Comparision of activities between neonates ($n = 21$) and anacondas of all sizes ($n = 514$) from a long-term study on their natural history (Rivas et al., 2007b). Main differences are the higher percentage of neonates found eating and the obvious lack of mating by neonates.

engaged in activities that made them more detectable such as moving, eating, and basking (Fig. 3).

The notion that opportunistic observations of neonates misrepresents their activity is supported by the telemetry observations, which suggest far higher frequency of being under vegetation and a considerably lower feeding frequency. Our telemetry study suggests that the odds of detecting an animal are lower than 20%, even if we knew where the animal was (Table 1). Low feeding frequency was also found by Pizzatto et al. (2009) with *L. fuscus*. They found only two feeding events while following ten neonates for seven months. The true feeding frequency in neonates probably falls somewhere between the high rate suggested by animals found in the act of constricting prey, which likely overestimate the actual feeding rate, and the low rate found by telemetry data that likely underestimate it. A low feeding frequency is also supported by the low growth rate found in wild-caught animals.

Average prey size observed in neonates is on par with the expected prey size found in adult snakes (Greene, 1992; Sazima, 1992), and it is not uncommon for large constrictors (Branch and Haacke, 1980; Rivas, 1998, 2000; Shine et al., 1998). Andreadis and Burghardt (2005) reported that neonatal Northern Water Snakes (*Nerodia sipedon*), given the choice, chose meal sizes close to 25% of their body mass. This is very close to the relative prey size found in wild neonatal anacondas. We do find a high variance in their diet with some neonates taking prey as large as 42% of their body (Table 2). This is perhaps due to their sit-and-wait strategy that probably deems them dependent on whatever prey comes within range.

Mobility and habitat use.—Some of the neonates' transmitter implantation incisions had not healed at the end of the study period, so the possibility exists that this may have influenced the observed behavior. However, we do not believe that the superficial wounds had a significant influence on the behavior of neonates or data collected for several reasons: none of the wounds showed any sign of infection; wild anacondas regularly show very large wounds as a consequence of predation attempts, from which they recover well (Rivas et al., 2007b); and the behavior found in radio-tagged anacondas (hiding regularly in underwater vegetation, using borrow pits with shallow water, etc.) did not differ from that found in wild-caught neonates. Anacondas with open

wounds are often found basking long hours (Rivas, pers. obs.). Radio-tagged neonates did not show any of these behaviors.

Neonatal anacondas were frequently (54%) found under plant cover in borrow pits with shallow, stagnant water. This is comparable with the 60% frequency with which adult anacondas use the same kind of habitat (Rivas et al., 2007b). However, we believe that these data underestimate the actual frequency with which both adults and neonates use these habitats due to detection biases. In fact, telemetry data suggest a much higher frequency.

Radio-tagged neonates did not move much during the time they were followed, resulting in a considerable overlap of individual home ranges. This low mobility is consistent with mark–recapture observations, where the only two recaptured neonates were found in exactly the same place as the original capture. Neonatal anacondas fall within the size classes of many adult snakes of other species, yet the average distance traveled in one day and the home range area are both much smaller than reported for other snakes. Larger home ranges than those found in neonatal anacondas occur with other neonatal species such as the rather sedentary Eastern Massasauga Rattlesnake (*Sistrurus catenatus catenatus*; Jellen and Kowalski, 2007). This is remarkable because home range is associated with body size (Schoener, 1981), and neonatal anacondas, exceeding 200 g, are more than one order of magnitude larger than neonatal Massasaugas (at 9.6 g). Northern Water Snakes (*N. sipedon*), with a comparable aquatic ecology, also show much larger home ranges than neonatal anacondas (Tiebout and Cary, 1987; Brown and Weatherhead, 1999a, 1999b; Pattishall and Cundall, 2009). The home range found is also very small compared with other large-sized tropical constrictors such as Carpet Pythons (*Morelia spilota*; Pearson et al., 2005), Puerto Rican Boas (*Epicrates inornatus*; Puente-Rolón and Bird-Picó, 2004), and Boa Constrictors (*Boa constrictor*; Holtzman et al., 2007). Neonatal anacondas also have small home ranges compared with other tropical, more closely related taxa that also live primary in aquatic ecosystems such as Water Pythons (Pizzatto et al., 2009). This low mobility, however, is consistent with the behavior of adult anacondas (Rivas, 2000) and with the emerging picture of neonatal anacondas suffering very high predation.

The predation of two of the radio-tagged neonates (see Cassie and Ingrid on Table 2) could be associated with a high risk of mortality associated with dispersal (Bonnet et al., 1999). We speculate that female anacondas might hedge their bets in these unpredictable habitats by producing animals with different strategies. If the conditions are favorable for more active individuals (e.g., fewer predators), active animals might be more successful, while more sedentary animals will do better in areas with strong predation. Selection for one or the other in the first months of life will influence what proportion of adult individuals will have a given strategy in a particular habitat. We believe that selection in this habitat favors neonates having less active foraging modes.

Social behavior and aggregations.—Wild anacondas frequently aggregate in a few ponds or cave-like depressions, but whether these are actual social aggregations or just aggregations around a limiting physical resource by animals that tolerate each other is uncertain. In our studies of the wild population at the peak of the dry season, we once found 34 anacondas smaller than 2 m SVL in a drying pond that was

barely 400 m^2 (Rivas, unpubl. data.). Studies are currently underway to determine the level of relatedness between these individuals. However, the variance in size suggests that they are not likely to be from the same clutch. Neonatal snakes are known to aggregate and appear to show a preference to congregating with conspecifics (Burghardt, 1983; Gillingham, 1987). Reiserer et al. (2008) reported thermal benefits of aggregations for neonatal Sidewinder Rattlesnakes (*C. cerastes*).

As the first study on the neonatal biology of any South American boid, and only the second on neonates of any large snake, we have barely broken ground in the understanding of the neonatology of Green Anacondas. What we have found supports the conclusion that neonates appear to closely resemble adults in several aspects of their ecology, including habitat preferences, mobility, prey size, and even growth rate.

ACKNOWLEDGMENTS

LITERATURE CITED

Andreadis, P. T., and G. M. Burghardt. 2005. Unlearned appetite controls: watersnakes (*Nerodia*) take smaller meals when they have the choice. Journal of Comparative Psychology 119:304–310.

Balaguera-Reina, S. A., M. Venegas-Anaya, O. I. Sanjur, H. A. Lessios, and L. D. Densmore. 2015. Reproductive ecology and hatchling growth rates of the American Crocodile (*Crocodylus acutus*) on Coiba Island, Panama. South American Journal of Herpetology 10:10–22.

Bonnet, X., G. Naulleau, and R. Shine. 1999. The dangers of leaving home: dispersal and mortality in snakes. Biological Conservation 89:39–50.

Branch, W. R., and W. D. Haacke. 1980. A fatal attack on a young boy by an African Rock python (*Python sebae*). Journal of Herpetology 14:305–307.

Brown, G. P., and P. J. Weatherhead. 1999a. Demography and sexual size dimorphism in northern water snakes, *Nerodia sipedon*. Canadian Journal of Zoology 77:1358–1366.

Brown, G. P., and P. J. Weatherhead. 1999b. Female distribution affects mate searching and sexual selection in male water snakes (*Nerodia sipedon*). Behavioral Ecology and Sociobiology 47:9–16.

Burghardt, G. M. 1977. Of iguanas and dinosaurs: social behavior and communication in neonate reptiles. American Zoologist 17:177–190.

Burghardt, G. M. 1983. Aggregation and species discrimination in newborn snakes. Zoological Tierpsychology 61:89–91.

Burghardt, G. M. 1992. Prior exposure to prey cues influences chemical prey preference and prey choice in neonatal garter snakes. Animal Behaviour 44:787–789.

Burghardt, G. M., H. W. Greene, and A. S. Rand. 1977. Social behavior in hatchling green iguanas: life at a reptile rookery. Science 195:689–691.

Burghardt, G. M., and M. A. Krause. 1999. Plasticity of foraging behavior in gartersnakes (*Thamnophis sirtalis*) reared on different diets. Journal of Comparative Psychology 113:277–285.

Burghardt, G. M., D. G. Layne, and L. Konigsberg. 2000. The genetics of dietary experience in a restricted natural population. Psychological Science 11:69–72.

Calder, W. A., III. 1996. Size, Function, and Life History. Dover Publications Inc., Mineola, New York.

Calle, P., J. A. Rivas, M. Muñoz, J. B. Thorbjarnarson, E. Dierenfeld, W. Holmstrom, E. Braselton, and W. Karesh. 1994. Health assessment of free-ranging anacondas (*Eunectes murinus*) in Venezuela. Journal of Zoo and Wildlife Medicine 25:53–62.

Calle, P. P., J. A. Rivas, M. C. Muñoz, J. B. Thorbjarnarson, W. Holmstrom, and W. B. Karesh. 2001. Infectious disease serologic survey in free-ranging Venezuelan anacondas (*Eunectes murinus*). Journal of Zoo and Wildlife Medicine 32:320–323.

Cobb, V., J. J. Green, T. Worrall, J. Pruett, and B. Glorioso. 2005. Initial den location behavior in a litter of neonates *Crotalus horridus* (Timber Rattlesnakes). Southeastern Naturalist 4:723–730.

Congdon, J. D., M. J. Pappas, J. D. Krenz, B. J. Brecke, and M. Schlenner. 2015. Compass orientation during dispersal of freshwater hatchling Snapping Turtles (*Chelydra serpentina*) and Blanding's Turtles (*Emydoidea blandingii*). Ethology 121:538–547.

Dunham, A. E., D. B. Miles, and D. N. Reznick. 1994. Life history patterns in squamate reptiles, p. 441–552. *In:* Biology of the Reptilia: Defense and Life History. Vol. 16. C. Gans and R. B. Huey (eds.). Branta Books, Ann Arbor, Michigan.

Gillingham, J. C. 1987. Social behavior, p. 184–209. *In:* Snakes: Ecology and Evolutionary Biology. R. A. Siegel, J. T. Collins, and S. S. Novak (eds.). McGraw-Hill, New York.

Gove, D., and G. M. Burghardt. 1975. Responses of ecologically dissimilar populations of the water snake, *Natrix s. sipedon*, to chemical cues from prey. Journal of Chemical Ecology 1:25–40.

Greene, H. W. 1992. The ecological and behavioral context for pitviper evolution, p. 107–117. *In:* Biology of Pitvipers. J. A. Campbell and E. D. Brodie (eds.). La Selva, Tyler, Texas.

Greene, H. W., G. M. Burghardt, B. A. Dugan, and A. S. Rand. 1978. Predation and defensive behavior of green iguana (Reptilia, Lacertilia, Iguanidae). Journal of Herpetology 12:169–176.

Greene, H. W., D. L. S. Hardy, J. Sciturro, and T. Farrel. 2002. Parental behavior in vipers, p. 179–205. *In*: Biology of the Vipers. G. W. Schuett, M. Höggren, M. E. Douglas, and H. W. Greene (eds.). Eagle Mountain Publishing, Eagle Mountain, Utah.

Gregory, P. T., L. A. Isaac, and R. A. Griffiths. 2007. Death feigning by grass snakes (*Natrix natrix*) in response to handling by human "predators." Journal of Comparative Psychology 121:123–129.

Herzog, H. A., Jr., and G. M. Burghardt. 1986. The development of antipredator responses in snakes: I. Defensive and open-field behaviors in newborns and adults of three species of garter snakes (*Thamnophis melanogaster, T. sirtalis, T. butleri*). Journal of Comparative Psychology 100:372–379.

Hilty, S. L. 2003. Birds of Venezuela. Princeton University Press, Princeton, New Jersey.

Holycross, A. T., and J. D. Fawcett. 2002. Observations on neonatal aggregations and associated behaviors in the Prairie Rattlesnake, *Crotalus viridis viridis*. The American Midland Naturalist 148:181–184.

Holtzman, D., S. Shifley, and D. Sisson. 2007. Spatial ecology of resident and displaced Boa constrictors *(Boa constrictor imperator)* on Ometepe island, Nicaragua: implications for conservation, p. 364–372. *In:* Biology of Boas, Pythons. R. W. Henderson and R. Powell (eds.). Eagle Mountain Publishing, Eagle Mountain, Utah.

Howze, J. M., K. M. Stohlgren, E. M. Schlimm, and L. L. Smith. 2012. Dispersal of neonate Timber Rattlesnake (*Crotalus horridus*) in the Southeastern Coastal Plain. Journal of Herpetology 46:417–422.

Ibañez, A., and R. C. Vogt. 2015. Chemosensory discrimination of conspecifics in the juvenile yellow-spotted river turtle (*Podocnemis unifilis*). Behaviour 152:219–230.

Jellen, B. C., and M. J. Kowalski. 2007. Movement and growth of neonate eastern Massasaugas (*Sistrurus catenatus*). Copeia 2007:994–1000.

Lamonica, R. C., H. Abrahão-Charles, M. F. C. Loguercio, and O. Rocha-Barbosa. 2007. Growth, shedding and food intake in captive *Eunectes murinus* (Linnaeus, 1758) (Serpentes: Boidae). International Journal of Morphology 25:103–108.

Mackessy, S. P., K. Williams, and K. G. Ashton. 2003. Ontogenetic variation in venom composition and diet of *Crotalus oreganus concolor*: a case of venom paedomorphosis? Copeia 2003:769–782.

Madsen, T., and R. Shine. 2000. Silver spoons and snake body sizes: prey availability early in life influences long-term growth rates of free-ranging pythons. Journal of Animal Ecology 69:952–958.

Morafka, D. J. 1994. Neonates: missing links in the life history of North American tortoises, p. 161–173. *In:* Biology of North American Tortoises. R. B. Bury and D. J. Germano (eds.). U.S. Fish and Wildlife Service, Research Report 13, Washington, D.C.

Morafka, D. J., E. K. Spangenberg, and V. A. Lance. 2000. Neonatology of reptiles. Herpetological Monographs 14: 353–370.

Mori, A., and G. M. Burghardt. 2008. Comparative experimental tests of natricine antipredator displays, with special reference to the apparently unique displays in the Asian genus, *Rhabdophis*. Journal of Ethology 26:61–68.

Mushinsky, H. R., and K. H. Lotz. 1980. Chemoreceptive responses of two sympatric water snakes to extracts of commonly ingested prey species: ontogenetic and ecological considerations. Journal of Chemical Ecology 6:523–535.

Nagy, K. A. 2000. Energy cost of growth in neonate reptiles. Herpetological Monographs 14:378–387.

Pattishall, A., and D. Cundall. 2009. Habitat use by synurbic watersnakes (*Nerodia sipedon*). Herpetologica 65: 183–198.

Pearson, D., R. Shine, and A. Williams. 2005. Spatial ecology of a threatened python (*Morelia spilota imbricata*) and the effects of anthropogenic habitat change. Austral Ecology 30:261–274.

Pike, D. A., L. Pizzatto, B. A. Pike, and R. Shine. 2008. Estimating survival rates of uncatchable animals: the myth of high juvenile mortality in reptiles. Ecology 89:607–611.

Pizzatto, L., T. Madsen, G. G. Brown, and R. Shine. 2009. Spatial ecology of hatchling water pythons (*Liasus fuscus*) in tropical Australia. Journal of Tropical Ecology 25:181–191.

Placyk, J. S., and G. M. Burghardt. 2005. Geographic variation in the frequency of scarring and tail stubs in eastern gartersnakes (*Thamnophis s. sirtalis*) from Michigan, USA. Amphibia–Reptilia 26:353–358.

Puente-Rolón, A., and F. Bird-Picó. 2004. Foraging behavior, home range, movements and activity patterns of *Epicrates inornatus* (Boidae) at Mata de Plátano Reserve in Arecibo, Puerto Rico. Caribbean Journal of Science 40:343–352.

Putman, N. F., and K. L. Mansfield. 2015. Direct evidence of swimming demonstrates active dispersal in the sea turtle "Lost Years." Current Biology 25:1221–1227.

Raphael, B. L., P. P. Calle, W. Karesh, J. A. Rivas, and D. Lawson. 1996. Technique for surgical implantation of transmitters in snakes. Proceedings of the Wildlife Disease Association 1996:82.

Reiserer, R. S., G. W. Schuett, and R. L. Earley. 2008. Dynamic aggregations of newborn sibling rattlesnakes exhibit stable thermoregulatory properties. Journal of Zoology 274:277–283.

Rivas, J. A. 1998. Predatory attack of a green anaconda (*Eunectes murinus*) on an adult human. Herpetological Natural History 6:158–160.

Rivas, J. A. 2000. Life history of the green anaconda (*Eunectes murinus*), with emphasis on its reproductive biology. Unpubl. Ph.D. diss., University of Tennessee, Knoxville, Tennessee.

Rivas, J. A. 2004. *Eunectes murinus* (green anaconda): subduing behavior. Herpetological Review 35:66–67.

Rivas, J. A. 2007. Conservation of anacondas: how Tylenol conservation and macroeconomics threaten the survival of the world's largest snake. Iguana 14:10–21.

Rivas, J. A. 2008. What is the length of a snake? Contemporary Herpetology 2008:1–3.

Rivas, J. A. 2010. Is wildlife management business or conservation—a question of ideology. Reptiles and Amphibians 17:112–115.

Rivas, J. A., and G. M. Burghardt. 2001. Sexual size dimorphism in snakes: wearing the snake's shoes. Animal Behaviour 62:F1–F6.

Rivas, J. A., and S. J. Corey. 2008. *Eunectes muriunus* (Green Anaconda). Longevity Herpetological Review 39:469.

Rivas, J. A., and L. Levin. 2002. Sex differential antipredator behavior in juvenile green iguanas, *Iguana iguana*: evidence for fraternal care, p. 119–126. *In:* Behavior, Diversity, and Conservation of Iguanas. A. C. Alberts, R. L. Carter, W. K. Hayes, and E. P. Martins (eds.). University of California Press, Berkeley.

Rivas, J. A., M. d. C. Muñoz, G. M. Burghardt, and J. B. Thorbjarnarson. 2007a. Mating system and sexual size dimorphism of the Green Anaconda (*Eunectes murinus*), p. 461–473. *In:* Biology of Boas, Pythons, and Related Taxa. R. W. Henderson and R. Powell (eds.). Eagle Mountain Publishing, Eagle Mountain, Utah.

Rivas, J. A., M. d. C. Muñoz, J. B. Thorbjarnarson, G. M. Burghardt, W. Holmstrom, and P. Calle. 2007b. Natural

history of the Green Anacondas in the Venezuelan llanos, p. 128–138. *In:* Biology of Boas, Pythons, and Related Taxa. R. W. Henderson and R. Powell (eds.). Eagle Mountain Publishing, Eagle Mountain, Utah.

Rivas, J. A., M. d. C. Muñoz, J. B. Thorbjarnarson, W. Holmstrom, and P. P. Calle. 1995. A safe method for handling large snakes in the field. Herpetological Review 26:138–139.

Rivas, J. A., and R. Y. Owens. 2000. *Eunectes murinus* (green anaconda). Cannibalism. Herpetological Review 31:45–46.

Rivas, J. A., R. Y. Owens, and P. P. Calle. 2001. *Eunectes murinus*: juvenile predation. Herpetological Review 32: 107–108.

Rivas, J. A., J. V. Rodriguez, and C. G. Mittermeier. 2002. The Llanos, p. 265–273. *In:* Wilderness. R. Mittermeier (ed.). Cemex, Mexico.

Rivas, J. A., J. B. Thorbjarnarson, R. Y. Owens, and M. d. C. Muñoz. 1999. *Eunectes murinus*: caiman predation. Herpetological Review 30:101.

Savitzky, B. A., and G. M. Burghardt. 2000. Ontogeny of predatory behavior in the aquatic specialist snake, *Nerodia rhombifer*, during the first year of life. Herpetological Monograph 14:401–419.

Sazima, I. 1992. Natural history of the jararaca pitviper, *Bothrops jararaca*, in southern Brazil, p. 199–216. *In:* Biology of Pitvipers. J. A. Campbell and E. D. Brodie, Jr. (eds.). La Selva, Tyler, Texas.

Schoener, T. W. 1981. An empirically based estimate of home range. Theoretical Population Biology 20:281–325.

Shine, R. G., P. S. Harlow, J. S. Keogh, and Boeadi. 1998. The influence of sex and body size on food habits of a giant tropical snake, *Python reticulatus*. Functional Ecology 12: 248–258.

Tiebout, H. M., and J. R. Cary. 1987. Dynamic spatial of the watersnake *Nerodia sipedon*. Copeia 1987:1–18.

Waters, R. M., and G. M. Burghardt. 2013. Prey availability influences the ontogeny and timing of chemoreception-based prey shifting in the striped Crayfish Snake, *Regina alleni*. Journal of Comparative Psychology 127:49–55.

Werner, D. I., E. M. Baker, E. d. C. Gonzalez, and I. R. Sosa. 1987. Kinship recognition and grouping in hatchling green iguanas. Behavioral Ecology and Sociobiology 21: 83–89.

White, G. C., and R. A. Garrot. 1990. Analysis of Wildlife Radio Tracking Data. Academic Press Inc., San Diego.

White, J. M., and J. A. Rivas. 2003. *Paleosuchus trigonatus* (Dwarf Caiman) Neonate time budget. Herpetological Review 34:141.

Willson, J. D., C. T. Winne, and M. B. Keck. 2008 Empirical tests of biased body size distributions in aquatic snake captures. Copeia 2008:401–408.

Wray, K. P., M. J. Margres, M. Seavy, and D. R. Rokyta. 2015. Early significant ontogenetic changes in snake venoms. Toxicon 96:74–81.