
POPULATION DEMOGRAPHY OF *RHINOCEMYS FUNEREA* (BLACK RIVER TURTLE) AT A PROTECTED FOREST RESERVE IN COSTA RICA

BRIAN FOLT

*Alabama Cooperative Fish and Wildlife Research Unit, 3301 School of Forestry and Wildlife Sciences,
Auburn University, Auburn, Alabama 36849, USA, e-mail: brian.folt@gmail.com*

Abstract.—*Rhinoclemmys funerea* (Black River Turtle) is a widely distributed and abundant freshwater aquatic turtle in the Caribbean lowlands of Central America, but little research has examined population ecology of the species. Here I used mark-recapture techniques to describe population demographics, morphological variation, and natural history of *R. funerea* from a stream in La Selva Biological Station, a forest reserve in northeastern Costa Rica. I built Jolly-Seber population models with the POPAN function to estimate sex-specific variation in apparent survival, capture, and entry probabilities and population size. Population structure was characterized by more adults than juveniles and a male-biased sex ratio. Mark-recapture population models estimated males to have much higher local apparent survival (0.75) than females (0.15), suggesting that females may be transient in local stream populations. Model-estimated population size also described males ($N = 35$; 95% Confidence Interval [CI] = 29–43) as more abundant than females ($N = 22$; 95% CI = 16–31) in the study area, but derived population estimates suggested that the female population varied substantially during the study. Adults were sexually dimorphic in mass, plastron length, and features of tail morphology. The results provide the first empirical estimates of survival, population size, and population structure for *R. funerea*. Because the study population occurred in a relatively undisturbed private reserve, the population parameters described at La Selva may serve as reference demographic conditions for *R. funerea* and may be used to understand how riparian land-use and habitat change influences turtles in Costa Rica.

Key Words.—apparent survival; La Selva Biological Station; mark-recapture; natural history; population size; sexual dimorphism

INTRODUCTION

Rhinoclemmys funerea (Black River Turtle; Fig. 1) is a semi-aquatic geoemydid turtle occurring in the Caribbean slopes of Central America from southern Honduras to central Panama (Savage 2002). Most research on *R. funerea* has been from Costa Rica, where the species occupies most freshwater habitats in Lowland Atlantic Moist and Wet forests (*sensu* Holdridge 1967), including large streams, rivers, tree swamps, ponds, and marshes (Savage 2002). The species is primarily aquatic and is most frequently observed swimming through habitat, basking on logs or adjacent low-gradient banks, or perched in shallow depths near the shore. *Rhinoclemmys funerea* is also known to occupy terrestrial habitats, where individuals forage for vegetation in riparian areas at the edge of water or in adjacent floodplain areas.

The best ecological studies of *R. funerea* have focused on the foraging ecology of the species in Tortuguero National Park, Costa Rica. Its diet includes the leaves and fruits of both aquatic and terrestrial plants (Moll and Jansen 1995): samples from stomach flushing indicated that Dumb Cane (*Dieffenbachia longispatha*) and *Panicum aquaticum* (no English common name)

were the most commonly eaten plants, while fecal samples suggested that *D. longispatha* and Threefork Morning Glory (*Ipomoea trifida*) may be the most commonly consumed seeds in Tortuguero (Jansen 1993; Moll and Jansen 1995). Because *R. funerea* defecates seeds capable of germination and the species occupies a variety of aquatic and terrestrial habitats, the species has been hypothesized to disperse seeds of terrestrial plants within and among habitats (Moll and Jansen 1995).

Despite having a relatively broad geographic distribution and being a fairly noticeable species in riparian habitats (e.g., the species basks conspicuously), *R. funerea* is an understudied species. Aside from studies of foraging ecology (Moll and Jansen 1995), no published studies have described basic structure of populations (e.g., population size or sex ratios) or estimated population demographic vital rates (e.g., survival). Because the species appears relatively abundant, reaches large body sizes, and occupies both aquatic and terrestrial habitats, the species may be an important component of terrestrial and freshwater aquatic communities throughout its range, but the scant ecological knowledge available for the species limits our understanding of the ecological role of this species in tropical forests.

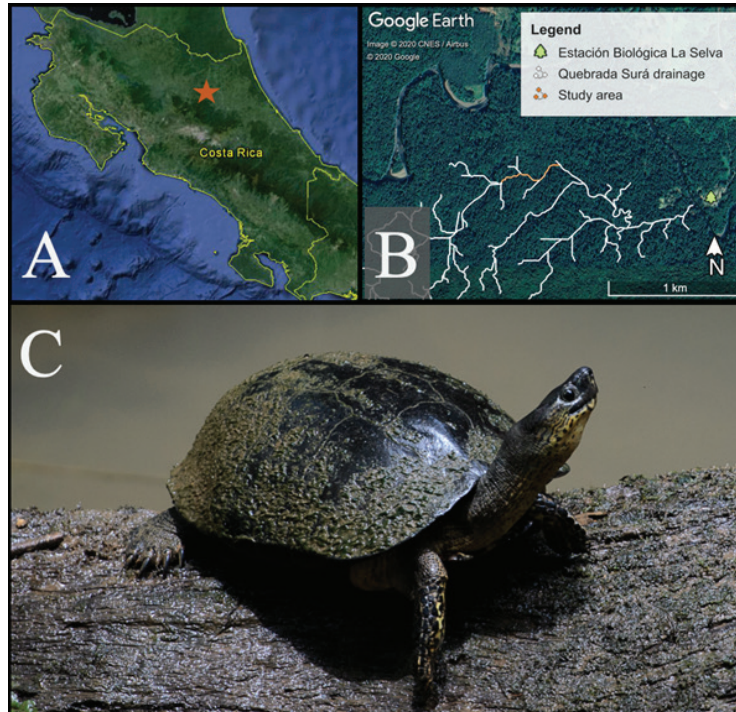


FIGURE 1. (A) Study area (orange star) in La Selva Biological Station (La Selva), Costa Rica. (B) La Selva, with white lines indicating the Quebrada Surá watershed and the orange line indicating the study site. (C) The study species, *Rhinoclemmys funerea* (Black River Turtle), basking in the Río Puerto Viejo within La Selva. (Satellite images are from Google Earth; C photographed by Jason Folt).

Given the lack of information available pertaining to *R. funerea*, the widespread destruction of Neotropical forest habitat (Bradshaw et al. 2009), including in the Caribbean lowlands of Central America (e.g., Costa Rica; Fagan et al. 2013), and the threatened status of turtles worldwide (Gibbons et al. 2000; Buhlmann et al. 2009), I undertook a population study of *R. funerea* at La Selva Biological Station in northeastern Costa Rica. My objective was to estimate basic population demographic parameters for *R. funerea*, such as population size, population structure, individual survival, and home range size. I used mark-recapture methods to repeatedly sample individuals through time and then built mark-recapture models that account for capture probability to estimate survival and population size. I also described sexually dimorphic morphological characters that can be used to identify sex and describe habitat use of individuals from the study population that have not been described for the species. Because La Selva Biological Station is a large protected reserve that is relatively undisturbed by humans, population demographic features at the site may serve as useful reference conditions for the ecology of the species in Costa Rica and elsewhere (Guyer 1994).

MATERIALS AND METHODS

Study species.—*Rhinoclemmys funerea* is a relatively large freshwater aquatic turtle, reaching maximum sizes

of 375 mm in midline carapace length (CL; Savage 2002). Both sexes become sexually mature at 200 mm plastron length, and females lay an average of 3.2 eggs per clutch (range, 1–6) with 1–4 clutches laid per season (Moll and Legler 1971). Examination of museum specimens suggested that adult *R. funerea* are sexually dimorphic in two features associated with reproduction: plastron concavity (concave for males; flat for females) and tail length (males have longer tails than females; Savage 2002).

Study site.—La Selva Biological Station (hereafter, La Selva) is a private reserve owned by the Organization for Tropical Studies (OTS; 10.42°N, 84.02°W) and is located in the Caribbean lowlands of northeastern Costa Rica. La Selva has an average temperature of 25.8° C, receives approximately 4,000 mm of rainfall annually (Sanford et al. 1994), and occurs within the Tropical Wet Forest of life zone system of Holdridge (Holdridge 1967; McDade and Hartshorn 1994). La Selva is 1,600 ha in area, of which 1,170 are old-growth forest, and elevation ranges from 30–135 m. Rainfall is seasonal at La Selva, with the increased precipitation May–December during the wet season and decreased precipitation from January to April during the dry season.

I conducted the present study in Quebrada Surá, a fourth-order stream that drains 4.8 km² of La Selva and the adjacent Braulio Carrillo National Park into the Río Puerto Viejo (Cadot and Wohl 2010). Quebrada Surá is

bordered by a variety of habitat types through La Selva, including primary forest, selectively logged forest, secondary forest, and abandoned plantations. I selected this stream as the study site because it is accessible, the study species appeared abundant therein (Guyer and Donnelly 2005), and the entire drainage occurs within protected forest reserves that are relatively unimpacted by humans. I collected turtles along an approximately 600 m stretch of Quebrada Surá, which parallels the Sendero Atajo trail (SAT) from where the SAT originates at the Lindero Occidental (LOC) trail (10.43320°N, 84.01399°W) to the 600 m marker on SAT (SAT 600; 10.43132°N, 84.01787°W; Fig. 1). The habitat is an alluvial primary forest floodplain: overstory tree species include Panama Rubber Tree (*Castilla elastica*), Almendro (*Dipteryx panamensis*), Gavilán (*Pentaclethra macroloba*), *Virola koschnyi* (no English common name), and Peruvian Almond (*Terminalia oblonga*), and the understory is dominated by palms (e.g., Amargo Palm, *Welfia regia*).

Sampling methods.—I collected turtles by hand encountered during standardized visual encounter surveys through the study area. These searches began at the LOC trail where it crosses Quebrada Surá and proceeded upstream along the south side of the creek. I systematically walked along the south side of the creek, and, whenever a turtle was observed basking, swimming, or foraging on land, I tried to catch the turtle by hand. I conducted 34 surveys that included a single thorough search of the entire study area from January 2014 to June 2015; I typically performed searches during the day from 1000–1600 ($n = 29$), but nocturnal searches (2000–2400) were performed on some occasions ($n = 5$). Additionally, I supplemented the dataset by making opportunistic hand captures in other areas downstream of the study area.

I performed surveys during periods of reduced rainfall and sunny conditions because these periods are characterized by decreased water levels, decreased turbidity, and increased basking behavior of *R. funerea*, conditions that may increase detection probability and capture success. The majority of surveys occurred during the dry season in January–May 2014 (21 surveys), but I also sampled in August–November 2014 (nine surveys) and June 2015 (four surveys) during periods of low rainfall. The entire study spanned a 17-mo period.

For each turtle captured, I identified individuals to sex and measured mass (g; 5 kg spring scale), midline carapace length (CL) and midline plastron length (PL; cm; ± 0.1) using calipers, and plastron-to-vent and tail length (cm; ± 0.1) using a ruler. I measured plastron-to-vent length to the center of the vent. I identified males by extending the tail and examining the relative distance the vent extended beyond the rear of the carapace and/or

by possessing a concave plastron (Guyer and Donnelly 2005). When possible, I recorded the capture location with a handheld GPS device, and I noted the behavior of the individual prior to capture. I marked each individual uniquely with a combination of marginal scute notches using a file. I recorded the behavior of individuals as: basking on shore or logs; foraging in water (visibly confirmed to be eating plants); perched in muck, shallow water, or shore; rooting in leaf-litter packs; swimming; or moving terrestrially in the floodplain. After collecting data, I released the turtles where they were captured.

Statistical analysis.—To understand common behavior of *R. funerea*, I summarized behavioral categories observed in the population. I tabulated mark-recapture encounter histories for each individual captured during sampling sessions in the study area, where individuals were seen (1) or not seen (0) during each survey. I used the Jolly-Seber (JS) model in program MARK (White and Burnham 1999) to analyze these encounter histories, because the population was open to demographic changes during the sampling period, such as emigration, immigration, and mortality, and because the JS model can be extended with the POPAN function to estimate population size. The POPAN model assumes that marked and unmarked turtles have equal capture probabilities, capture does not influence survival, marks are detected perfectly, and the study area remains constant in size. I removed juveniles from the analysis because I only observed six individuals in the study and I only recaptured one; I then focused on understand sex-specific differences in demographics of the adult population. I did not include opportunistic observations in the mark-recapture analysis, although I used those data in morphological analyses.

I built POPAN models using program MARK (White and Burnham 1999) through the RMark package (Laake 2013) in the statistical Program R (R Core Team 2018). To address whether the data violated JS model assumptions, I assessed structural goodness-of-fit (GOF) and overdispersion of data with the goodness-of-fit procedure in program RELEASE. Specifically, I tested whether marking influences the capture probability of individuals using test 2, a capture rate test of homogeneous catchability for marked and unmarked turtles that calculated a Pearson's Chi-square statistics for each group. I developed a set of *a priori* hypotheses to model how apparent survival probability (ϕ), capture probability (p), immigration ($pent =$ probably of entry), and population size (N) vary in relation to sex. The POPAN model estimates apparent survival probability, which is the probability of individuals both surviving and staying within the study area; this value is different from true survival probability, because individuals that are no longer present at sites are not

necessarily dead but may be alive and have emigrated to another area. Model construction was guided in an all-subsets framework, where the model set included all combinations of parameters varying or not by sex; this included a null model. I evaluated models using an information-theoretic approach for model selection with Akaike’s Information Criterion (AIC) adjusted for small sample sizes (AIC_c; Burnham and Anderson 2010). The AIC_c index was used as a measure of model parsimony (Burnham and Anderson 2010, where the models with lower values are most supported by the data. I ranked models by calculating the difference between the model with the lowest AIC_c and each other model (i.e., ΔAIC_c). I evaluated the likelihood that a model was the best fitting model in the model set by calculating model weight (w_i). To understand how N varies by season and sex, I averaged the derived estimates of N from among the full model set and evaluated it graphically.

Because sex-biased dispersal is common among vertebrates with males frequently being greater dispersers and having larger home ranges than females (Dobson 1982; Dubey et al. 2008; Johansson et al. 2008), I predicted that males would have larger home ranges than females. I plotted geographic locations for all individuals captured two or more times on Google Earth and calculated the observed maximum home range size for individuals along Quebrada Surá using a shapefile with the path of the stream (Fig. 1). I tested whether males have larger observed maximum home range size than females using a Generalized Linear Model with a Poisson distribution.

I tested whether males and females varied in body size (CL) using a linear model (i.e., Student’s *t*-test). I tested whether males and females varied in mass, tail length, plastron-to-vent length, and carapace-plastron length relationship using dummy-coded multivariable linear models where a response variable was tested against a linear x-variable, a dummy-coded variable for sex, and an interaction term between the linear x-variable and sex (i.e., Analysis of Covariance). I first built full models with three parameters (linear x-variable, sex, and interaction) and then used a backwards elimination approach for model selection: if the interaction term was non-significant, it was removed and a more simple, two parameter model was built (linear x-variable, sex). All linear models were built in Program R (R Core Team 2018). I used appropriate tests to confirm assumptions of normality and homoscedasticity before fitting linear models, with $\alpha = 0.05$. The data and R scripts from this paper are available on GitHub (<https://github.com/brianfolt/river-turtle-demography>).

RESULTS

I made 108 observations of 50 individuals in the study area. Individuals were captured an average of 2.2

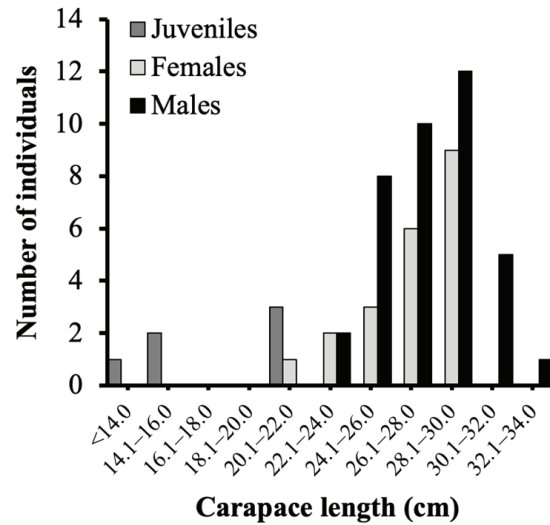


FIGURE 2. Body size distribution (midline carapace length; cm) of juvenile, female, and male *Rhinoclemmys funerea* (Black River Turtles) from a fourth-order stream at La Selva Biological Station, Costa Rica, 2014–2015.

times (range, 1–8); 48% of individuals were recaptured at least once. I also made 22 additional captures of 21 individuals during opportunistic searches downstream of the study area, including two individuals that I also observed within the study area. The total sample of individuals included six juveniles, 21 females, and 38 males (Fig. 2). The observed adult sex ratio was 1M:0.56F, which differed significantly from 1M:1F ($\chi^2 = 4.898$, $df = 1$, $P = 0.027$). Individuals were most frequently captured when swimming (36% of observations), perched on shore (18%) or in the shallows (17%), or foraging in the floodplain forest (10%; Fig. 3).

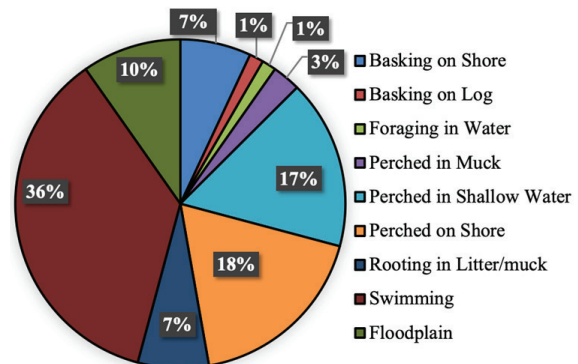


FIGURE 3. Observed behavior in a population of *Rhinoclemmys funerea* (Black River Turtle) at La Selva Biological Station, Costa Rica. The graph is based on 72 observations of 45 individuals. Basking indicates when the individual was sitting stationary in direct sun, while Perched indicates when environmental conditions were overcast and no strong, direct sunlight penetrated to the turtle. Rooting in Litter/muck indicates when a turtle was found swimming through a thick leaf-litter pack in the water, and Floodplain refers to individuals observed foraging terrestrially in floodplain forest.

TABLE 1. Number of parameters, Akaike's information criterion (AIC) corrected for small sample size (AIC_c), ΔAIC_c , and model weight (w_i) of models built to estimate apparent survival (ϕ), capture probability (p), probability of entry ($pent$), and population size (N) for adult *Rhinoclemmys funerea* (Black River Turtle) at La Selva Biological Station, Costa Rica. Dots (.) indicate when parameters were held constant; sex indicates modeled differences between males and females.

Model	k	AIC_c	ΔAIC_c	w_i
$\phi(\text{sex}) p(.) pent(.) N(.)$	5	563.70	0.00	0.36
$\phi(\text{sex}) p(\text{sex}) pent(.) N(.)$	6	565.83	2.13	0.12
$\phi(\text{sex}) p(.) pent(.) N(\text{sex})$	6	565.92	2.22	0.12
$\phi(\text{sex}) p(.) pent(\text{sex}) N(.)$	6	565.95	2.25	0.12
$\phi(\text{sex}) p(\text{sex}) pent(.) N(\text{sex})$	7	567.97	4.27	0.04
$\phi(\text{sex}) p(\text{sex}) pent(\text{sex}) N(.)$	7	568.07	4.37	0.04
$\phi(\text{sex}) p(.) pent(\text{sex}) N(\text{sex})$	7	568.12	4.41	0.04
$\phi(.) p(\text{sex}) pent(.) N(.)$	5	568.15	4.45	0.04
$\phi(.) p(.) pent(.) N(.)$	4	568.54	4.84	0.03
$\phi(.) p(\text{sex}) pent(\text{sex}) N(.)$	6	569.44	5.74	0.02
$\phi(.) p(.) pent(.) N(\text{sex})$	5	570.05	6.35	0.02
$\phi(\text{sex}) p(\text{sex}) pent(\text{sex}) N(\text{sex})$	8	570.32	6.62	0.01
$\phi(.) p(\text{sex}) pent(.) N(\text{sex})$	6	570.40	6.70	0.01
$\phi(.) p(.) pent(.) N(\text{sex})$	5	570.70	7.00	0.01
$\phi(.) p(\text{sex}) pent(\text{sex}) N(\text{sex})$	7	571.41	7.71	0.01
$\phi(.) p(.) pent(\text{sex}) N(\text{sex})$	6	571.85	8.15	0.01

Goodness-of-fit testing indicated that capture-recapture data met the assumption of homogeneous catchability between marked and unmarked turtles ($\chi^2 = 12.67$, $df = 34$, $P = 0.986$). The most well supported model among the model set described ϕ varying by sex and other demographic parameters as sex invariant (Table 1). Estimates described female survival ($\phi = 0.15$; 95% CI = 0.03–0.55) as lower than male survival ($\phi = 0.75$; 95% CI = 0.26–0.96). Capture probability of individuals was 0.07 (95% CI = 0.06–0.11). Model-estimated super-population sizes suggested a larger population of males ($N = 35$; 95% CI = 29–43) than females ($N = 22$; 95% CI = 16–31) in the study area. Derived estimates of N described considerable intersexual variance in population size during the study period, with female abundance decreasing toward zero at the site during the study period (Fig. 4). Aside from the best supported model, the second, third, and fourth-best models described ϕ and p as varying by sex, ϕ and N as varying by sex, and ϕ and $pent$ as varying by sex, respectively. These models received $\Delta AIC_c > 2.00$, however, and model weight suggested that the best supported model was about three times more likely to be the true best model among the model set.

Maximum home range size of males (mean = 150.2 \pm 1.2 [standard error] m; 95% CI = 120.9–186.6; $n = 15$) was larger than that of females (mean = 50.1 \pm 1.1

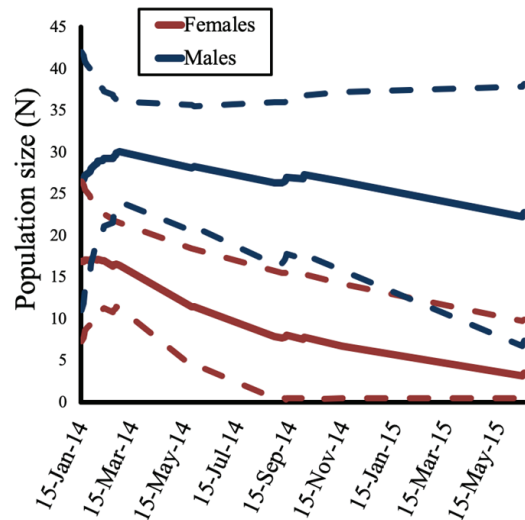


FIGURE 4. Model-averaged derived estimates of population size (N) for female and male *Rhinoclemmys funerea* (Black River Turtle) in a 600 m stretch of a fourth-order stream at La Selva Biological Station, Costa Rica, January 2014 to June 2015.

m; 95% CI = 45.1–55.6; $n = 7$), which was a significant difference ($Z = 19.12$, $df = 21$, $P < 0.001$). Mean CL of males (27.8 ± 0.68 ; 95% CI = 27.2–29.9; range, 23.5–34.4; $n = 38$) was larger than females (27.1 ± 0.55 ; 95% CI = 26.0–28.1; range, 20.3–30.0; $n = 21$), but this difference was not significant ($Z = 1.07$; $df = 1$, 57; $P = 0.289$). Allometric relationships between mass and PL varied by sex and CL. Females were an average of 269.6 g (95% CI = 140.6–398.6) heavier than males across all values of CL ($Z = 4.23$; $df = 2$, 39; $P < 0.001$). Body mass of both sexes increased by 270.4 g (95% CI = 245.0–295.9) with each unit increase in CL ($Z = 21.52$; $df = 2$, 39; $P < 0.001$; Fig. 5). The allometric relationship between CL and PL also varied by sex and CL. Female plastrons were an average of 1.56 cm (95% CI = 1.20–1.92) larger than male plastrons across all values of PL ($Z = 8.66$; $df = 2$, 56; $P < 0.001$), and PL of both sexes increased by 0.76 cm (95% CI = 0.69–0.83) with each unit increase in CL ($Z = 21.77$; $df = 2$, 56; $P < 0.001$; Fig. 5).

Allometric relationships between tail length and plastron-to-vent length also varied by sex and CL. Male tails were 1.89 cm (95% CI = 1.38–2.41) longer than female tails across all values of CL ($Z = 5.40$; $df = 2$, 28; $P < 0.001$), and tail length of both sexes increased by 0.23 cm (95% CI = 0.14–0.32) with each unit increase in CL ($Z = 7.58$; $df = 2$, 28; $P < 0.001$; Fig. 6). Similarly, the plastron-to-vent length of males was 1.71 cm (95% CI = 1.33–2.08) larger than females across all values of CL ($Z = 4.51$; $df = 2$, 28; $P < 0.001$), and plastron-to-vent length of both sexes increased by 0.14 cm (95% CI = 0.08–0.21) with each unit increase in CL ($Z = 9.20$; $df = 2$, 28; $P < 0.001$; Fig. 6).

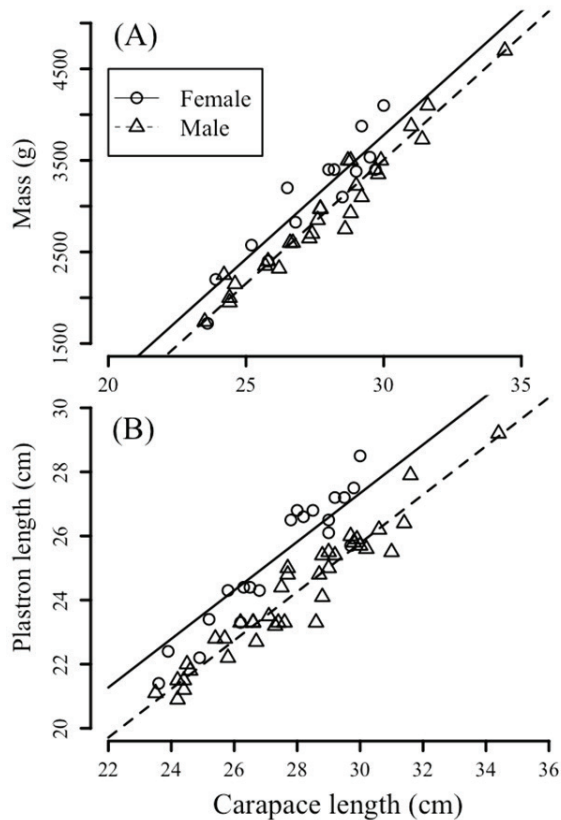


FIGURE 5. Relationship of (A) carapace length and mass and (B) carapace length and plastron length for adult *Rhinoclemmys funerea* (Black River Turtle) at La Selva Biological Station, Costa Rica.

DISCUSSION

Here I estimated population demographic features of *R. funerea* in a protected forest reserve to better understand the population ecology and life history of this little-studied species. Observed and estimated population structure was male-biased and observed home ranges were greater for males than females. Female apparent survival in the local population ($\phi = 0.15$) was much lower than that of males ($\phi = 0.75$) during the 17-mo study period. While the study duration was relatively short for demographic studies of turtles, these results suggest that males may form relatively large home ranges that are more permanent in fourth-order streams, while females may occupy smaller home ranges for short periods of time before emigrating to occupy other habitats. Because the watershed of La Selva is a series of streams that drain into the Río Puerto Viejo and the Río Sarapiquí, population dynamics of *R. funerea* at La Selva may best be described as a series of stream populations that are connected by dispersal in a metapopulation context.

I observed a male-biased sex ratio in the study population, and mark-recapture models suggested that

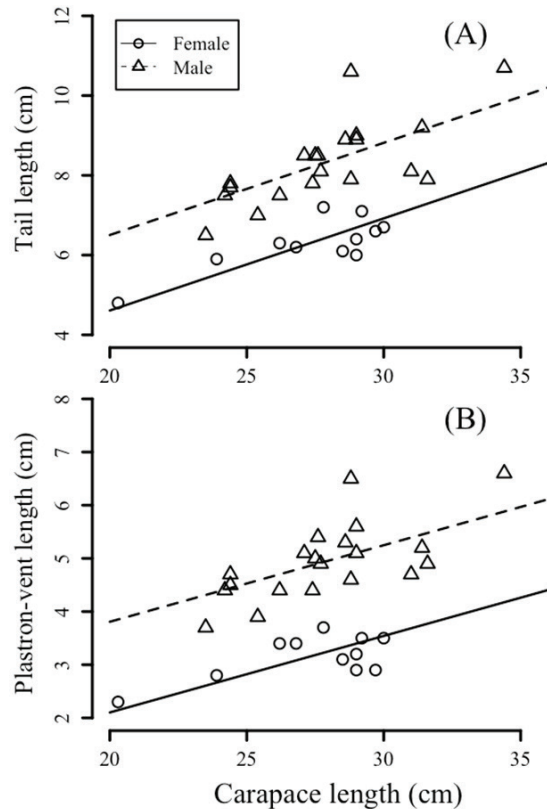


FIGURE 6. Relationship between (A) carapace length and tail length and (B) plastron-to-vent length for adult *Rhinoclemmys funerea* (Black River Turtle) at La Selva Biological Station, Costa Rica.

the sex ratio increased in disparity during the study. This result is similar to a population of *R. funerea* at Tortuguero that was also male-biased (1.87M:1.00F; Jansen 1993). While biased sex ratios are not uncommon in turtle populations, uneven ratios can be due to sampling biases resulting from collecting techniques, behavioral differences between the sexes, and/or different ages of sexual maturity (Gibbons 1990). I used analytical methods that estimate population structure while accounting for sex-specific variation in detection, such that the estimated sex ratio may reflect a true greater abundance of males than females in the study population during the study period. Curiously, I failed to detect any females in the population during four surveys on consecutive days in June 2015, and male-bias in the sex ratio was estimated to increase during the study. Analyses removing the June 2015 samples still estimated a declining number of females in the local population (unpubl. data). Because nesting occurs from March to August (Acuña 1993), females may become less common in the study area because they temporarily emigrate to other areas more favorable for nesting conditions, such as larger rivers with open beaches for nesting.

My results confirm previous morphological examinations of sexually dimorphic characters (e.g., tail length, plastral concavity) while adding plastron length as an additional character useful for identifying sex of *R. funerea*. In general, plastral concavity was useful to identify males to sex; however, two individuals (233 mm and 244 mm CL) both had a flattened plastron that was suggestive of the female sex, but possessed long tails with the cloacae extending well beyond the rear of the carapace. Given the tail morphology, I identified these individuals as males, and I suggest that future researchers might most effectively identify subadult sex using multiple measures, including plastral length, tail length, and plastron-to-vent length in addition to plastral concavity.

Rhinoclemmys funerea are known to frequently use terrestrial habitat to forage for plants, particularly at night (Ernst and Barbour 1989). I often observed *R. funerea* to use terrestrial habitat in areas with gently sloping banks that may allow easy access to floodplain habitats for terrestrial foraging. In terms of foraging locations, I most often saw individuals foraging terrestrially in floodplain forest habitats, but I frequently detected individuals when they were rooting through mucky, leaf-litter packs underwater. While it is unclear why *R. funerea* occupy the leaf-litter packs, they seem to be actively using those microhabitats and I suspect they may use leaf-litter packs as feeding grounds for aquatic invertebrates. Future studies with larger sample sizes could seek to understand behavioral variation among age classes and sexes of *R. funerea*.

Juveniles were uncommonly observed in the study area, and among six juveniles captured during surveys, only one was recaptured. Previous research at Tortuguero National Park found that hatchling *R. funerea* in their first year of life were largely terrestrial before moving to occupy aquatic habitat, and that juveniles appeared to mostly occupy lentic habitats before moving to lotic habitats as subadults (Jansen 1993). At La Selva, juveniles may be uncommonly captured because they are more abundant in other habitats that I did not survey and only present in small numbers in Quebrada Surá, and/or difficult to detect (Garcés-Restrepo et al. 2019). Crocodylians are thought to be the primary natural predator of *R. funerea* by consuming juveniles and also occasionally adults (Savage 2002; Guyer and Donnelly 2005), and smaller juveniles may avoid using larger stream habitats to decrease predation risk from crocodylians. Among a sample of 59 adults observed at La Selva, four males and one female were missing a limb appendage (8.5% of individuals observed), and the shell of one individual was extremely chipped, pocked, and scarred. Both of these features may be a consequence of attempted predation events by *Caiman crocodylus* (Spectacled Caiman), a species commonly

observed in the study area (including large individuals >1.5 m total length).

In other areas of Costa Rica and Central America, *R. funerea* may also be predated by humans. Acuña (1993) reported that some indigenous communities in Costa Rica use *R. funerea* during religious rituals and eat adults. Additionally, individuals in rural, non-indigenous communities may also hunt and consume *R. funerea* occasionally; however, because La Selva is a protected forest reserve with limited or nonexistent poaching of turtles, population processes are mostly driven by natural causes of mortality at the site. For these reasons, the population structure and vital rates of *R. funerea* observed at La Selva may serve as reference demographic conditions to understand how contemporary threats to biodiversity may influence freshwater turtle species. Habitat loss and fragmentation is rampant where *R. funerea* occurs in the Caribbean versant of Costa Rica (Fagan et al. 2013), and riparian forest conversion to agriculture can have negative effects on aquatic turtle communities (Sterrett et al. 2011), particularly species that frequently uses terrestrial landscapes like *R. funerea*. Future research might seek to understand how riparian land use influences the population ecology of *R. funerea* by comparing population demographics at La Selva to other disturbed habitats in the area (Guyer et al. 1994).

I made observations of *R. funerea* occupying space in aggregations that have led me to suspect that the species may be much more social than previously understood. During one notable instance in January 2014 during clear water conditions, I observed > 10 *R. funerea* in a pool of Quebrada Surá, where the individuals were swimming together in a close group (i.e., schooling). They were moving lazily around each other in approximate circles and seemed more intent on interacting with other individuals than any other functional activity. Similarly, while juveniles were rarely observed, the observations I made suggested social behavior for that age class as well. On 13 June 2015, I captured three juveniles that were basking within about 25 cm of each other on a gently sloping shoreline of Quebrada Surá. Two individuals were small and may have been of similar ages (13.9 cm CL, 14.5 cm CL), while the third was larger (20.6 cm CL). That three of six total juveniles encountered during the study were found aggregated together suggests some degree of sociality or schooling behavior for juveniles and that such schooling behavior may be independent of age. Together, these observations suggest that *R. funerea* may interact with conspecifics in social contexts much more than has been previously appreciated (but see Merchan-Fornelino 2003). Future research should seek to understand the causes and consequences of social behavior in *R. funerea*.

Acknowledgments.—I was supported by an Organization for Tropical Studies Graduate Research Fellowship (Christiane and Christopher Tyson and Dole Food fellowships) and a Young Explorer’s Grant from the National Geographic Society during data collection. I conducted the study under the guidelines and permission of Auburn University IACUC 2010-1827 and the Costa Rican government (MINAET Resolución 009-2014-SINAC). I thank Craig Guyer, John David Curliss, and Michelle Thompson for helping catch turtles, Diego Dierick for lending a scale, Jason Folt for providing a photograph of the study species, and Nicholas Marzolf for providing a GIS shapefile. This paper is contribution no. 935 of the Auburn University Museum of Natural History.

LITERATURE CITED

- Acuña, R. 1993. Las Tortugas Continentales de Costa Rica. Universidad de Costa Rica, San José, Costa Rica.
- Bradshaw, C.J., N.S. Sodhi, and B.W. Brook. 2009. Tropical turmoil: a biodiversity tragedy in progress. *Frontiers in Ecology and the Environment* 7:79–87.
- Buhlmann, K.A., T.S.B. Akre, J.B. Iverson, D. Karapatakis, R.A. Mittermeier, A. Georges, A. G. Rhodin, P.P. van Dijk, and J.W. Gibbons. 2009. A global analysis of tortoise and freshwater turtle distributions with identification of priority conservation areas. *Chelonian Conservation and Biology* 8:116–149.
- Burnham, K.P., and D.R. Anderson. 2010. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. 2nd Edition. Springer-Verlag, New York, New York, USA.
- Cadol, D., and E. Wohl. 2010. Geomorphology wood retention and transport in tropical, headwater streams, La Selva Biological Station, Costa Rica. *Geomorphology* 123:61–73.
- Dobson, F.S. 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Animal Behavior* 30:1183–1192.
- Dubey, S., G.P. Brown, T. Madsen, and R. Shine. 2008. Male-biased dispersal in a tropical Australian snake (*Stegonotus cucullatus*, Colubridae). *Molecular Ecology* 17:3506–3514.
- Ernst, C.H., and R. Barbour. 1989. *Turtles of the World*. Smithsonian Institution Press, Washington D.C., USA.
- Fagan, M.E., R.S. DeFries, S.E. Sesnie, J.P. Arroyo, W. Walker, C. Soto, R.L. Chazdon, and A. Sanchun. 2013. Land cover dynamics following a deforestation ban in northern Costa Rica. *Environmental Research Letters* 8:034017. <https://iopscience.iop.org/article/10.1088/1748-9326/8/3/034017/meta>
- Garcés-Restrepo, M.F., J.L. Carr, and A. Giraldo. 2019. Long-term variation in survival of a Neotropical freshwater turtle: habitat and climatic influences. *Diversity* 11:1–12.
- Gibbons, J.W. 1990. Sex ratios and their significance among turtle populations. Pp. 171–182 *In* Life History and Ecology of the Slider Turtle. Gibbons, J.W. (Ed.). Smithsonian Institution Press, Washington, D.C., USA.
- Gibbons, J.W., D.E. Scott, T.J. Ryan, K.A. Buhlmann, T.D. Tuberville, B.S. Metts, J.L. Greene, T. Mills, Y. Leiden, S. Poppy, and C.T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. *BioScience* 50:653–656.
- Guyer, C. 1994. The reptile fauna: diversity and ecology. Pp. 210–216 *In* La Selva: Ecology and Natural History of a Neotropical Rain Forest. McDade, L.A. K.S. Bawa, H. Hespeneheide, and G.S. Hartshorn (Eds.). University of Chicago Press, Chicago, Illinois, USA.
- Guyer, C., and M. Donnelly. 2005. Amphibians and Reptiles of La Selva, Costa Rica, and the Caribbean Slope. University of California Press, Berkeley, California, USA.
- Holdridge, L. 1967. Life Zone Ecology. Tropical Science Center, San José, Costa Rica.
- Jansen, K.P. 1993. Ecology of the tropical freshwater turtle *Rhinoclemmys funerea* in Caribbean Costa Rica. M.Sc. Thesis, Southwest Missouri State University, Springfield, Missouri. 56 p.
- Johansson, H., Y. Surget-Groba, and R.S. Thorpe. 2008. Microsatellite data show evidence for male-biased dispersal in the Caribbean lizard *Anolis roquet*. *Molecular Ecology* 17:4425–4432.
- Laake, J.L. 2013. RMark: an R interface for analysis of capture-recapture data with MARK. Alaska Fisheries Science Center, Seattle, Washington, USA.
- McDade, L.A., and G.S. Hartshorn. 1994. La Selva Biological Station. Pp. 6–14 *In* La Selva: Ecology and Natural History of a Neotropical Rain Forest. McDade, L.A. K.S. Bawa, H. Hespeneheide, and G.S. Hartshorn (Eds.). University of Chicago Press, Chicago, Illinois, USA.
- Merchan-Fornelino, M. 2003. Contribución al conocimiento de la biología de la Tortuga Negra (*Rhinoclemmys funerea*) y la Tortuga Roja (*R. pulcherrima manii*) en Costa Rica. Ph.D. Dissertation, Universidad Complutense de Madrid. 328 p.
- Moll, D., and K.P. Jansen. 1995. Evidence for a role in seed dispersal by two tropical herbivorous turtles. *Biotropica* 27:121–127.
- Moll, D., and J. Legler. 1971. The life history of a neotropical Slider Turtle, *Pseudemys scripta* (Schoepff) in Panama. *Bulletin of the Los Angeles County Museum of Natural History Science* 11:1–102.

Herpetological Conservation and Biology

- R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.r-project.org/>.
- Sanford, R., P. Paaby, J. Luvall, and E. Phillips. 1994. Climate, geomorphology, and aquatic systems. Pp. 19–33 *In* La Selva: Ecology and Natural History of a Neotropical Rain Forest. McDade, L.A. K.S. Bawa, H. Hespeneide, and G.S. Hartshorn (Eds.). University of Chicago Press, Chicago, Illinois, USA.
- Savage, J.M. 2002. The Amphibians and Reptiles of Costa Rica: A Herpetofauna Between Two Continents, Between Two Seas. University of Chicago Press, Chicago, Illinois, USA.
- Sterrett, S.C., L.L. Smith, S.W. Golladay, S.H. Schweitzer, and J.C. Maerz. 2011. The conservation implications of riparian land use on river turtles. *Animal Conservation* 14:38–46.
- White, G.C., and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46:120–138.



BRIAN FOLT is a Post-doctoral Researcher in the Alabama Cooperative Fish and Wildlife Research Unit at Auburn University, Auburn, Alabama, USA. Brian is interested in understanding demographic processes that influence population growth of vertebrates (particularly amphibians and reptiles) and using such information to guide conservation and wildlife management in decision-support contexts. He received his B.S. from Ohio University, Athens, Ohio, USA, and his Ph.D. from Auburn University, where at both institutions he studied the population regulation of amphibians and reptiles in Costa Rica. (Photographed by Jason Folt).