age annual nesting rate of 25% based on radio-collared adult females. Taylor et al. (1991) reported that 25.4% of 370 adult female alligators killed in 1987 had nested. In contrast, Joanen and McNease (1980) reported that 63% of 25 adult female alligators examined at Rockefeller Refuge in Louisiana from April–August 1969 were productive. However, many females listed by Joanen and McNease (1980) as productive were actually vitellogenic females collected in April and May that may not have laid eggs, even if not disturbed (Taylor et al., 1991).

Twelve of the 15 radio-collared female alligators in Lacassine Pool had larger home ranges and greater daily movement during the spring breeding season than during any other season of the year. Of these 12, only two eventually nested. This suggests that increased activity during spring relates to more than just breeding behavior. Chabreck and Joanen (1979) noted that alligators in southern Louisiana do not feed during winter and feed at reduced rates during the months of October and March. The resumption of normal feeding activity along with the more moderate temperatures of spring, as compared to the relatively high temperatures of summer and early fall and cool temperatures of winter, may combine to stimulate alligator activity during the spring season.

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Effect of Habitat on Survival of Eggs and Sex Ratio of Hatchlings of *Caiman crocodilus yacare* in the Pantanal, Brazil

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ABSTRACT.—Flooding of nests and predation were identified as the major mortality agents of eggs of *Caiman crocodilus yacare* in Brazil. Nests on floating grass mats and in forests were flooded in 1989, but only floating grass mats nests were flooded in 1990. Predation on eggs was high in forest nests, but my presence may have increased predation. No nest on floating grass mats was attacked by predators.

The period of sex determination of *C. c. yacare* can extend to 40 d of incubation. I predicted nest temperature with a multiple regression model incorporating weather variables during incubation. The predicted nest temperatures for nests on floating grass mats and nests in forest were correlated with the sex ratio of the clutch. High nest temperatures (> 31.5 C) produced mostly males, and low nest temperatures (< 30.5 C) produced only females. The estimated sex ratio varied between years in nests on floating grass mats, but not in forest nests. Estimated nest temperatures significantly affected the snout-vent lengths of hatchlings but not their masses. Fifty percent of nesting occurred on floating grass mats, so the destruction of this habitat by introduced animals such as the water buffalo (*Bubalus bubalis*) will adversely affect the productivity and hence long-term density of caimans in the Pantanal.

Rates of survival of crocodilians vary among sizes and probably habitats (Abercrombie, 1989). Inundation and predation are the main causes mortality of crocodilian eggs. In the Pantanal, *Caiman crocodilus yacare* nests in forests and floating grass mats (Breyer and Pott, pers. comm.). In the north of the Pantanal, nests are attacked by *Nasua nasua* (Procionidae) and inundation also causes mortality of eggs (Crawshaw and Schaller, 1980; Cintra, 1988).

The sex of crocodilians is determined by incubation temperature, which, in turn, is influenced by the location of the nests (Ferguson and Joanen, 1982, 1983; Lang et al., 1989). Nest temperatures also affect the probability of embryo survival by influencing embryonic development and hence the amount of time that eggs are vulnerable to inundation and predation (Webb and Smith, 1984). The temperature of nests, the sex ratio, and the incubation period of five species of the subfamily Crocodylidae and three species of Alligatoridae are functions chiefly of when and where eggs are laid (Lang et al., 1989). Temperatures inside nests are affected by insolation, rainfall, air temperature, and by metabolic heat of embryos (Webb et al., 1977, 1983; Magnusson, 1979; Ferguson and Joanen, 1983).

Incubation temperature affects the sex ratio of species differently. Low temperatures produce females and high temperatures produce males in *Alligator mississippiensis* (Ferguson and Joanen, 1983), *Paleosuchus trigonatus* (Magnusson et al., 1990), *Caiman crocodilus* (Lang et al., 1989), *Crocodylus niloticus* (Hutton, 1987) and *Crocodylus siamensis* (Lang, 1987). However, for *Crocodylus johnstoni, Crocodylus porosus* (Webb and Smith, 1984; Webb and Cooper-Preston, 1989), and *Crocodylus palustris* (Lang et al., 1989), females are produced at low and high temperatures and males are produced at intermediate temperatures. In *Alligator mississippiensis, Crocodylus porosus,* and *Crocodylus johnstoni,* sex "determined" at high temperatures can to be reversed up to 40 d of incubation (Webb and Manolis, 1987; Deeming and Ferguson, 1989).

In this study, I attempted to answer the following questions: 1) Do mortality rates of eggs differ between nests in forests and floating grass mats? 2) Do changes in air temperature and rainfall affect the incubation temperature of eggs? 3) Is the sex ratio of hatchlings related to the incubation temperature? 4) Does the sex ratio of hatchlings vary between habitats? 5) Does incubation temperature affect the length and weight of hatchlings?

MATERIALS AND METHODS

The study was conducted on Nhumirim Ranch (18°59'S and 56°39'W), which is in a region of perched lakes (Mourão et al., 1988) and Campo Dora Ranch (18°55'S and 56°39'W), which is in a region of intermittent rivers and grasslands subject to flooding.

I searched for nests in January and February of 1989 and 1990. I found forest nests from

TABLE 1. Mortality of eggs from forest and nests of floating grass mat nests at Nhumirim, and Campo Dora Ranches, in 1989 and 1990.

	Attacked by predators	Flooded	Total
Nhumirim			
1989			
Forest	23	4	50
Floating grass	0	6	42
1990			
Forest	38	0	40
Floating grass	0	0	49
Campo Dora			
1989			
Forest	12	5	17
Floating grass	0	2	15
1990			
Forest	8	0	15
Floating grass	0	2	5

horseback or on foot. Nests on floating grass mats were located from an ultralight aircraft. I mapped the positions of all nests and observed the condition of nests at the end of February and March. I measured the temperatures at the center of nests and collected one egg from each nest to estimate its age based on an age/size table for *C. c. yacare* embryos (Crawshaw, 1989). I used an ARBA thermometer to measure nest temperature.

In 1990, temperatures of three nests on floating grass mats and three forest nests were measured every six hours for 10–15 d. Wire mesh fences were erected around forest nests to impede access by predators.

In 1989, I artificially incubated eggs from five forest nests, and in 1990 I artificially incubated eggs from ten forest nests and eleven floating grass mat nests. In each year I removed the eggs to the laboratory at estimated ages between 30–60 d. In 1989 I captured 10 to 15 hatchlings from each of 21 nests in floating grass mats and 20 forest nests within one week of hatching. I measured, weighed, and sexed these and hatchlings incubated in the laboratory in 1990. I determined the sex of all hatchlings by surgery (Magnusson and Hero, 1990).

The critical period during which temperature determines the sex of *Alligator mississippiensis* is from the seventh to the fortieth day of incubation (Deeming and Ferguson, 1989). However, it was not practicable to measure incubation temperature between 7 and 40 d of incubation for the majority of my caiman nests. I measured temperature at intervals of six hours

between 5 and 30 d of incubation for three forest nests and three floating grass mat nests. For 34 additional forest nests and 44 additional floating grass mat nests, I measured temperature once between the second and third week of incubation. To estimate temperatures for these 78 nests, I used regression models that predicted nest temperature from daily measurements of air temperature, rainfall, time of day, and age of nest. I considered deviations from this relationship as the best estimate of the unique effects of nests, independent of weather effects. Using the regression coefficients and estimated unique nest effects from the daily model, and the mean ambient temperatures during the critical period (7–40 d), I estimated the mean temperature for each nest during the critical period.

RESULTS

Many forest nests were attacked by predators on both ranches in both years. No nest on floating grass mats was attacked by predators in 1989 or 1990 (Table 1). The difference in the proportion of nests attacked by predators was statistically significant ($x^2 = 34.23$, df = 1, P < 0.001). I visited eight nests in the forest in 1990, and the next day all had been attacked by predators, suggesting that my presence increased predation. I observed *Cerdocyon thous* eating eggs from two nests and I found tracks and feces of *Nasua nasua* and *Sus scrofa* near 15 nests which had been destroyed by predators.

In 1989, rainfall was intense (814 mm) from January to March, and both forest and floating grass mat nests were flooded. In 1990, rainfall was less intense (362 mm), and only two floating grass mat nests were flooded (Table 1). There was no statistically significant difference between habitats in the proportion of the nests flooded ($x^2 = 0.02$, df = 1, P = 0.95).

The variation of temperature within forest nests was 5 C (Fig. 1A–C), and 6 C within floating grass mat nests (Fig. 1D–F), between the second and third weeks of incubation.

Multiple regression was used to relate temperatures in 78 nests to the air temperature, rainfall, time of day, and nest effects. For 44 floating grass mat nests, I obtained the best prediction of the temperature by a model that used time of day, mean air temperature, and rainfall one day before the temperature reading (Table 2). The model explained 56% of the variance in nest temperature. Temperatures of 34 forest nests were best predicted by time of day, mean air temperature during the three days before the reading, and rainfall during the seven days before the reading (Table 3). The relationship between rainfall during the previous seven days and the temperature of nests was parabolic, and was modeled as a quadratic function. The model

explained approximately 52% of the variation in nest temperatures. Floating grass mat nests apparently responded more to weather variation over a short interval (one day) and forest nests responded to weather variation over a longer interval (3–7 d). I used the models to predict mean nest temperatures between 7–40 d of incubation, and I related these to the sex of the hatchlings.

The critical period for sex determination extends up to 40 d. The 26 nests moved to the laboratory were incubated at 30 C. All nests taken to the laboratory at less than 40 d of incubation produced females (Fig. 2). Nests with high initial temperatures (>31.5 C) and taken to the laboratory at less than 40 d of incubation produced only females. However, nests with high initial temperatures that were older than 40 d produced males (Fig. 3).

The forest nests with estimated temperature less than 30.5 C produced 100% females. Between 30.5 C and 31.5 C forest nests produced about 10% males, and at temperatures greater than 31.5 C produced 80% to 100% males. The nests in floating grass mats with estimated temperatures less than 30.5 C produced 100% females. At estimated temperatures between 30.5 C and 31.5 C these nests produced about 15% males, and about 31.5 C they produced about 50% males (Fig. 4).

In 1989, I determined the sex ratio of hatchlings from 20 forest nests and 21 floating grass mat nests. In 1990, I estimated the sex ratio of hatchlings from four forest nests and seven floating grass mat nests that were taken to the laboratory after more than 40 d of incubation. For the majority of nests, I had an estimate of the temperature of incubation in the critical period but not the sex ratio of the hatchlings. To estimate the sex ratio in these nests, I predicted temperatures with the regression models then used the estimated temperatures to predict the sex ratio of hatchlings. The estimated sex ratio was similar between the two years in forest nests (Mann-Whitney $U_{36.26} = 422.00$, P = 0.250), but
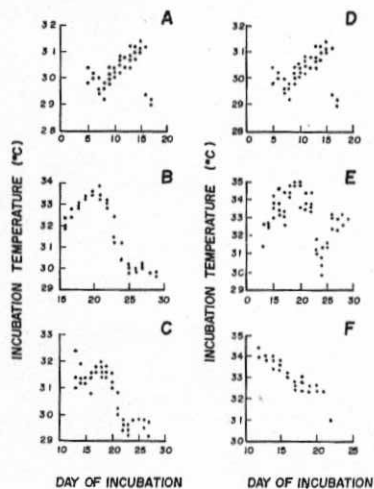

FIG. 1. Relationship between temperature of incubation and days of incubation in three nests of floating grass mats (A–C), and three nests in forests (D–F).

varied significantly (Mann-Whitney $U_{30.33} = 622.50$, P = 0.000) between years in nests on floating grass mats (Fig. 4A, B). The same results were obtained when I compared only nests in which I had determined the sex ratio of hatchlings by surgery (Mann-Whitney $U_{22.11} = 121.00$, P = 0.643 and $U_{20.11} = 210.5$, P = 0.000, respectively).

Hatchlings from nests with high estimated incubation temperatures were significantly longer than hatchlings from nests with lower temperatures (Fig. 5A). There was no significant effect of temperature on the mass of hatchlings (Fig. 5B), and on the length and mass of hatch-

TABLE 2. Significance of partial regressions of the variables mean temperature (T1) and rainfall (C1) one day before each reading of incubation temperature, and time of day (H) on incubation temperature of nests on floating grass mats.

Variable	df	SQ	MQ	F	P
Regression	3	71.661	23.887	14.099	0.000
Residual	33	55.909	1.694		

	Independent contributions of the variables (partial regressions)		
Variable	Coef.	t	P
Constant	6.223	1.534	0.134
T1	0.786	6.078	0.000
C1	0.060	2.188	0.036
H	0.240	3.030	0.000

TABLE 3. Significance of the partial regressions of the variables: mean air temperature 3 days before (T3) and rainfall (C7 and C7 · C7) during the seven days before each reading of temperature and time of day (H) on incubation temperature of forest nests.

Variable	df	SQ	MQ	F	P
Regression	4	76.614	19.154	10.927	0.000
Residual	40	70.118	1.753		
Independent contributions of the variable (partial regressions)					
Variable		Coef.		t	P
Constant		19.773		5.559	0.000
T3		0.271		2.366	0.023
C7		0.060		2.188	0.036
C7·C7		−0.002		−1.954	0.098
H		0.117		1.694	0.098

lings (Temp = 23.848 + 1.083 × length − 0.115 × weight, R^2 = 0.216, P = 0.161). However, this effect may be masked by differences in masses of hatchlings due to variation in the time between their hatching and weighing (up to one week).

DISCUSSION

Inundations caused by rainfall during the period of incubation killed embryos in floating grass mat nests and forest nests. Predators take many eggs in forest nests, but it was not possible to estimate the magnitude of natural predation because my presence near nests probably increased the rate of predation.

The temperatures in forest nests apparently respond to the effects of weather accumulated over three to seven days, and temperatures of floating grass mat nests apparently are affect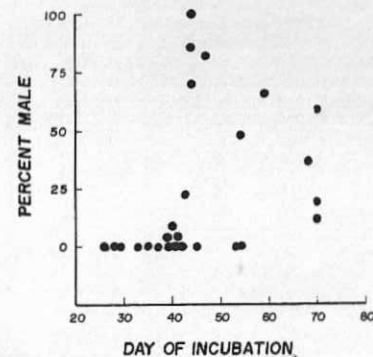ed more by conditions on the previous day. This difference may be due to differences in the exposure of nests to insolation.

Incubation temperature determines the sex of *Caiman crocodilus yacare*. Low temperatures (<30.5 C) produce females and high temperatures (>31.5 C) produce mainly males. This pattern is similar to that found by Lang et al. (1989) for *Caiman crocodilus crocodilus* in the laboratory. However, mean predicted temperatures did not predict the sex ratio of *C. c. yacare* with precision. This may be due simply to differences in the capacity of the models to predict mean temperature in the forest and in floating grass mats. However, it is possible that other factors influence the sex ratio. Bull (1985) showed that in addition to mean temperature, variability in temperature can affect the sex ratios of three species of turtles (*Graptemys*). Georges (1989)

FIG. 2. Relationship between sex ratio and day of incubation that nests were taken to laboratory for incubation at ±30 C.
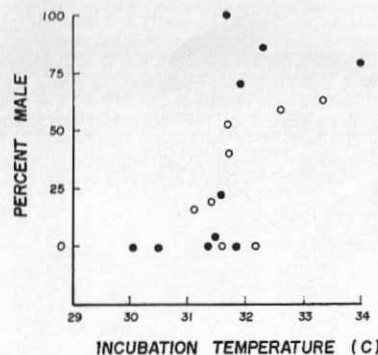
FIG. 3. Relationship between sex ratio and estimated temperature of forest nests (open circles) and floating grass mats (closed circles) with more than 40 d of incubation.
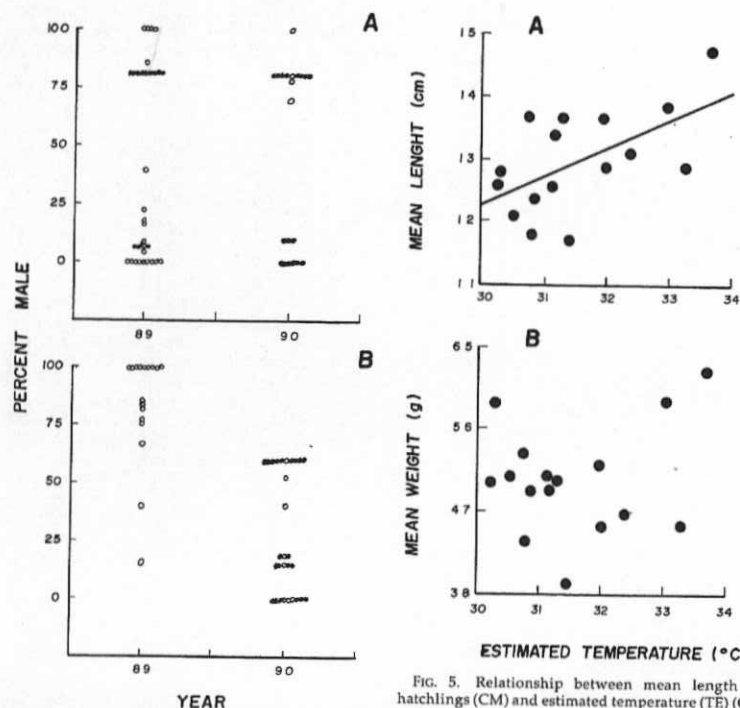
FIG. 4. Estimated (closed circles) and observed (open circles) sex ratios in nests in forests (A) and floating grass mats (B) in 1989 and 1990.

FIG. 5. Relationship between mean length of hatchlings (CM) and estimated temperature (TE) (CM = 1.261 + 0.453 × TE, r^2 = 0.332, P = 0.019, n = 16), and mean mass of hatchlings and estimated incubation temperature, (r^2 = 0.051, P = 0.402, n = 16).

suggested that the proportion of embryonic development that takes place above the critical temperature is more important than the mean temperature for sex determination. It was not possible to test this hypothesis with my data.

The sex ratio is influenced by nesting habitat, but the effect of habitat depends on weather condition. The estimated sex ratio varied little between years in forest nests, but, in floating grass mat nests, the sex ratio decreased from 81.57% males in 1989 to 30% males in 1990. The factors that lead females to select nesting habitats are unknown. However, it is probable that the cycle in the extent of flooding that occurs at intervals of 7.6 ± 5.2 years in Pantanal (Cadavid, 1984), will alter the availability of nesting habitat for caimans.
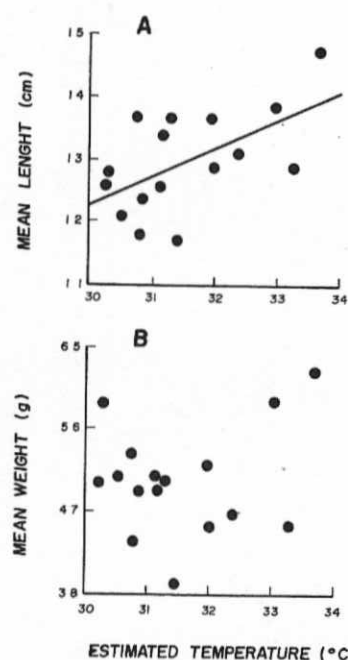
High temperatures produce more rapid em-

bryonic development at hatching of *Alligator mississippiensis* than do low temperatures (Deeming and Ferguson, 1989). Incubation temperature significantly affected the mean length, but not the mean weight of hatchlings of *C. c. yacare*. Individuals from warm nests (mainly males) should have larger initial sizes.

The extent of inundation in Pantanal influences the use of nesting habitats by *Caiman crocodilus yacare* (Campos, unpubl. data). The mortality of eggs depends on the nesting habitat. Rainfall directly affects survivorship of eggs through flooding and also affects nest temperature. This probably changes the sex ratio of individuals that will be recruited to the adult population.

About 50% of the nests in the lakes region (Nhecolandia) are on floating grass mats. This should be taken into account before the intro-

duction of buffalo (*Bubalus bubalis*), which are known to destroy floating grass mats in Australia (Hill and Webb, 1982). In some years, these nests produce the majority of female hatchlings. Changes in the proportions of nesting habitats can be expected to cause long term changes in the dynamics of the population. Therefore, the effects of habitat and weather must be considered in models of the population dynamics of *Caiman crocodilus yacare* in the Pantanal.

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Reproduction of the Timber Rattlesnake (*Crotalus horridus*) in the Appalachian Mountains

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ABSTRACT.—I studied the reproductive ecology of the timber rattlesnake (*Crotalus horridus*) during a 19-yr period in the Appalachian Mountains in NW Virginia and nearby areas. The short (5.3 mo) and cool active season places constraints on growth and reproduction. Gravid and postpartum females averaged 93 cm (76–112 cm) total length. Mating occurred in late summer (observations from 21 August to 18 September) coincident with the onset of follicular yolking. Ovulation took place in late May and early June of the following year. Postpartum females with litters were seen from 4 August to 16 October. The mean age of probable first-time reproducers was 7.8 yr (5–11 yr) with 7- and 8-yr-old females making up 56% of the first-time reproducers. I found a mean interval of 3.08 yr (2–4 yr) between successive reproductions for marked females. The proportion reproductive by age class ranged from 17% for 5-yr-olds to 66% for 10-yr-old and older females. The high proportion (60%) of the adult female sample reproductive during the year of capture is attributable to greater catchability of gestating females. Only 32% of the more-representative April-May sample was gravid. Because of vagaries of the weather and synchronization of the breeding cycle among females, reproduction occurred in pulses with the proportion of mature females reproducing estimated to range from 10–75% per year.

The timber rattlesnake (*Crotalus horridus*) is a characteristic secondary consumer in many of the eastern North American deciduous forests. Despite its widespread occurrence, there are few long-term studies and only in recent years have some aspects of its life history been documented. Gibbons (1972) and Keenlyne (1978) reported female size and fecundity in South Carolina and Wisconsin, respectively. Fitch (1985) reported on demography and reproduction in Kansas and reviewed *C. horridus* reproduction. Brown (1991, 1993) studied female reproductive ecology of the species in New York and thoroughly reviewed its literature and conservation biology.

Rattlesnakes in my study area hibernate for an average of 6.7 mo (5.7–7.5 mo) from October to late April or early May and may be exposed to cool, wet summers (Martin, 1992). Since little or no growth or maturation is expected to occur while rattlesnakes are in hibernation, the length of the active season is expected to be an important constraint on growth, maturation, and reproductive rates.

In 1973 I undertook a long-term field study of the timber rattlesnake in NW Virginia and adjacent areas. The purpose of this study was to describe age of female maturity, body size of adult females, length of the female reproductive cycle, frequency of reproduction, and an-

nual variations in the proportion of females reproducing. These data are necessary for a full understanding of the demographic life history of this widespread viperid snake.

METHODS

Study Area.—This study was carried out in Shenandoah National Park (hereinafter called Shenandoah) located in the Blue Ridge Mountains of Virginia (38–39°N, 78–79°W) and in other study sites located in NW Virginia, E West Virginia, W Maryland, and S Pennsylvania (37–40°N, 77–80°W) (cf. map in Martin, 1992). The study area contained 271 known denning colonies, but most of the sampling and recapture data came from 19 communal denning sites located as follows: Shenandoah (12), other parts of Virginia (3), West Virginia (1), Maryland (2), and Pennsylvania (1). The study area is located along the eastern edge of the unglaciated Appalachians about mid-way between the northern and southern limits of the timber rattlesnake's range within the Appalachians. The region is characterized by heavily wooded northeast–southwest trending ridges separated by agricultural valleys. The forested habitats of *C. horridus* are dominated by oaks (*Quercus* spp.) and exposed rock is uncommon in most sections.

Rattlesnake activity centers around communal overwintering dens (hibernacula) and nearby places used for gestation and parturition, herein termed "birthing rookeries." Such sites were generally located at elevations ranging from 200–1200 m, in or near ledges, scree, and