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Maternal Effects on Life-History Traits in the Amazonian Giant River Turtle *Podocnemis expansa*

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ABSTRACT.—Energy allocation to eggs and nest site selection by females can affect life-history variables such as offspring size, offspring number, developmental rate, survivorship, growth rate, and performance in oviparous reptiles. Nest site selection can affect offspring phenotype by altering incubation conditions. I present evidence of a positive effect of female size on clutch size, egg mass, and nest depth through the study of trackways left by female river turtles, *Podocnemis expansa*, on their nesting beaches. Larger females laid larger clutches composed of larger eggs, which were buried deeper than clutches laid by smaller females. The data suggest that *P. expansa* does not conform to optimal propagule size models. Neither egg size nor clutch size reached a plateau as female size increased. Females seem to allocate the extra energy (in absolute terms) gained allometrically with increasing size and age to both number and size of eggs. There was no evidence of a trade-off between egg size and number after removing the effect of female size. Larger eggs produced larger hatchlings that survived better but grew less than individuals of smaller initial size during the first two months of life, under unlimited food conditions. I suggest that fitness of female *P. expansa* increases by producing larger eggs because of the advantage that larger hatchlings have in survival. Deeper nests experience cooler temperatures and tend to produce a higher percentage of males than more superficial nests. Therefore, there is a potential for important effects of nest depth on sex ratios produced by different sized females within the population and possibly by single females throughout their lifetime. Constant temperature in artificial incubation experiments had an effect on the size of individuals at hatching, but differences vanished by the second month of age via the greater growth rate shown by individuals of smaller initial size.

Life-history variables such as offspring size, offspring number, developmental rate, survivorship, growth rate, and performance may be influenced by maternal factors such as energy allocation and nest site selection in oviparous reptiles. Because those parameters affect offspring fitness, females could maximize their own fitness by optimizing that of their offspring (Brockelman, 1975). On one hand, species with larger clutches and no parental care are expect-

ed to show the patterns of energy allocation predicted by optimality models (Smith and Fretwell, 1974), which may involve compromises between longevity and fertility, and trade-offs between offspring size and offspring number (Roff, 1992; Stearns, 1992; Bulmer, 1994; Sikes, 1998 and references therein). On the other hand, nest site selection can alter incubation conditions experienced by the offspring that can affect their phenotype (Shine and Harlow, 1996). Incubation conditions such as temperature vary with nest substrate characteristics, sun and wind exposure, and nest depth (Souza and Vogt, 1994; Janzen, 1994; Shine and Harlow, 1996). Incubation temperature has profound effects on

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reptiles, particularly for species with temperature-dependent sex determination (TSD). Females allocate energy to eggs and choose nest site locations within each reproductive season, and it has been suggested that certain combinations of both parameters (nest-site choice dependent on egg size) could be adaptive in turtle species (Roosenburg, 1996). Here, I report on the effects of female size of a freshwater turtle species (*Podocnemis expansa*) on egg size, egg number, and an aspect of nest location, namely, nest depth.

Podocnemis expansa is a large species inhabiting the Amazon and Orinoco basins in South America. The size of adult females ranges between 50 and 80 cm carapace length (Hildebrand et al., 1997). Descriptions of the nesting behavior in *P. expansa* report that females excavate a nest hole such that their head is level with the surface of the beach while ovipositing (Mosqueira-Manso, 1945; Ramírez, 1956; Vanzolini, 1967). Therefore, large females should dig deeper holes than smaller females. Ramírez (1956) suggested a positive relationship between female size and nest depth, but no data have been presented to test this prediction.

Podocnemis expansa exhibits temperature-dependent sex determination (TSD), such that males are produced at low incubation temperatures and females at high temperatures (Alho et al., 1985; Valenzuela et al., 1997). Females nest in sandbars where temperature varies considerably with depth in the nesting substrate (Valenzuela, 1999). An experimental study in the same nesting area revealed a significant effect of the depth of artificial nests on offspring sex ratio (Valenzuela, 1999). In general, the deeper the nest the cooler and less variable the incubation conditions, which tended to produce more males (Valenzuela, 1999). The experimental effect of nest depth on sex ratio would be of great importance if similar nest depth variation were present in the wild. Particularly, if nest depth is correlated with female size within the population, or within a given female as her size increases with age, then the population sex ratio or a female's lifetime sex-ratio production could be affected. These considerations are especially important given the endangered status of *P. expansa*.

Here, I describe significant size-related maternal effects on offspring fitness: clutch size, egg size, hatchling size, offspring survival, and offspring growth. I consider these results in the context of optimal propagule size theory. In addition, I explore another potentially important size-related maternal effect, the depth of nests and its associated thermal consequences. Field investigations are combined with a laboratory

study to explore how temperature affects offspring size, survival, and posthatching growth.

MATERIALS AND METHODS

The study was carried out at the Middle Caquetá River, Colombian Amazonia, at a region called Tamanco, which is comprised of the nesting beaches of Tamanco and Playa Roja (0°50.5'S, 71°48.7'W). *Podocnemis expansa* females nest on sandbars that become exposed as the level of the river falls during the dry season (September to February). Tamanco beach is an island sandbar, whereas Playa Roja beach is part of the southern bank of the Caquetá River; it is a higher beach than Tamanco beach.

Studies of size-related maternal effects require precise measurements of female size, which ideally are taken directly from the females. When *P. expansa* females are disturbed while nesting, they abort digging the nest hole or covering the eggs already deposited (Hildebrand et al., 1997). Because of the endangered status of this species, the local authorities from the indigenous peoples have prohibited disturbing nesting females, and hence no measurements of body size could be obtained directly. As an alternative methodology, I measured the width of the trackways left by females in the sand and used this width as an estimate of their carapace length. In a congeneric species (*P. unifilis*), trackway width is positively correlated with female body size measured as straight-line carapace length ($r^2 = 0.96$, $N = 101$, $P < 0.00001$; T. Escalona, unpubl. data). Therefore, although indirect, the use of trackway width as a proxy for female length is appropriate in this circumstance. Trackway width was measured to the nearest 0.5 cm as the distance between the outermost sides of the hind feet tracks. Measurements were made in relatively flat areas of the nesting beach, where the trackways were straight and the tracks were clear and consistent, that is, where width measurements were the same at 3–4 points along the trackway portion. The beaches were visited every morning to search for nests and for trackways left by females on the previous night. The data reported here correspond only to cases where it was possible to unambiguously assign the female's trackway to her nest.

Depth to the top egg and to the bottom egg in the egg chamber (nest depth) were measured to the nearest 0.5 cm following nest excavation. Five eggs per nest were selected at random and weighed to the nearest 0.1 g using a portable electronic balance. I found that five eggs was the sample size necessary to detect a 5% difference among nests with 95% certainty given the variance in egg mass (Sokal and Rohlf, 1995) de-

terminated by weighing 100 eggs from single nests (Hildebrand et al., 1997; this study).

Clutch size was determined in two ways. For some nests, the number of eggs was counted directly following nest excavation. For all remaining undisturbed nests, the number of eggs was recorded by adding the number of hatchlings, infertile eggs, and dead embryos found at the end of the incubation period. Nests of this last group had been marked after oviposition, monitored until the expected hatching date, and then excavated before emergence.

I used Model II regression (Sokal and Rohlf, 1995) to analyze the functional relationship between female length and clutch and egg size, as well as between egg size and hatchling size. Model II regression was used because these variables contain natural variation rather than being under experimental control, and because female size was measured indirectly, and was thus subject to additional measurement error. Because egg size and hatchling size are in the same units (grams), major axis regression was used (Sokal and Rohlf, 1995). In the case of female size versus clutch size, and female size versus egg mass, reduced major axis analysis was performed because the variables differed in their units of measurement (Sokal and Rohlf, 1995). The significance of all major axis or reduced major axis regressions was calculated with a randomization test.

To test for the existence of a trade-off between the number and size of the eggs, I removed the effect of female size from the relationship in two ways. First, I performed a multiple regression of clutch size against female size and egg size and analyzed the resulting regression of the number of eggs onto egg mass holding female size constant. Second, I analyzed the relationship of the residuals of the regression of clutch size on female size and of egg mass on female size (see Rowe, 1992).

Data used to assess the effect of egg size on hatchling size came from 19 nests monitored in the field, as well as three nests incubated in the laboratory. These 19 seminatural nests consisted of groups of 100 eggs placed inside a plastic mesh bag. The material of the bags allowed water drainage and gas exchange, whereas it reduced attacks by predatory crickets (Grillotellidae) and prevented the mixing of emerging hatchlings from different nests (Valenzuela, 1999). Hatchlings from field nests were collected just before emergence after they had absorbed the residual yolk, and they were weighed and measured. Curved-line carapace length and curved-line width were recorded from field hatchlings to the nearest 0.1 cm at the time of emergence using a flexible tape measure. Straight-line measurements were taken from

laboratory hatchlings to the nearest 0.1 cm at the time of emergence and at two months of age using a Vernier caliper. Hatchlings produced in the lab were provisioned ad libitum during those two months. Measurements were taken with a tape measure in the field because a replacement Vernier caliper was not available by the emergence time of the hatchlings. Hatchling mass was recorded for all hatchlings to the nearest 0.1 g at the time of emergence using an electronic balance. In the laboratory experiments, eggs from the three nests were distributed uniformly among four temperatures (30.5°C, 32.5°C, 33.5°C, and 34.5°C) to minimize clutch effects. Hatchling sex was determined by radioimmunoassay (RIA) of testosterone levels in the blood, a nondestructive method that gives accurate information on sex determination for this species (Lance et al., 1994; Valenzuela et al., 1997).

Average egg mass from each clutch was used when initial egg size was included in any of the following analyses. I tested for morphological differences (in body mass, length, and width) among hatchlings produced at the four constant incubation temperatures using a Multivariate Analysis of Covariance (MANCOVA; Renchir, 1995) to account for the possible effects of sex and initial egg mass on the relationship between temperature and hatchling size. Morphological data at time of emergence (body mass, length, and width) from hatchlings that died during their first two months of life were compared to data from surviving individuals using a MANCOVA to include the effect of initial egg mass and mean incubation temperature. Hatchling growth was calculated for laboratory individuals only, as the difference between carapace length and width measurements taken at two months of age and at time of emergence. A MANCOVA was used to investigate the effect of size at emergence (length and width) on growth of individuals (in length and width) using initial egg mass, incubation temperature, and sex as covariates. Standard normal deviates (Sokal and Rohlf, 1995) of all morphological variables (size at hatching and growth) were used in all the MANCOVA tests. All statistical tests were conducted in JMP (SAS Institute, 1995) and BIOMstat 3.2c (Rohlf and Slice, 1999).

RESULTS

Descriptive statistics of the variables measured in the field (mean, standard deviation, range, and sample size) are presented in Table 1. As expected, I found a positive relationship between female trackway size and clutch size. Large females tended to lay a larger number of eggs than did small females (Table 2). I also found a positive relationship between clutch

TABLE 1. Descriptive statistics of life-history variables of *Podocnemis expansa* from the Caquetá River, Colombia. SD = standard deviation. * a value of 0 corresponds to one nest where the first eggs found were located at the surface of the beach, uncovered.

Variable	Mean	SD	Range	N
Female size index (cm)	54.8	4.3	44–66	88
Egg mass (g)	41.8	4.4	24.9–51.9	112
Clutch size (# eggs)	103.1	23.7	50–184	153
Total clutch mass (g × 10 ³)	4.4	1.3	1.79–7.23	84
Depth first egg (cm)	24.7	9.2	0*–52	120
Depth last egg (cm)	46.0	8.5	21–71	143
Hatchling mass field (g)	27.9	2.2	20.6–33.4	605
Curve-line hatchling length (cm)	5.7	0.2	4.2–6.5	605
Curve-line hatchling width (cm)	6.1	0.2	5–6.9	605
Hatchling mass lab (g)	24.8	4.0	20–30	62
Straight-line hatchling length (cm)	5.5	0.7	4.5–7.2	62
Straight-line hatchling width (cm)	4.5	0.3	3.9–5	62

size and nest depth: deep nests contained larger clutches (Table 2, Fig. 1A). Furthermore, larger females dug deeper nests (Table 2). Female size and clutch size were both positively correlated with average egg mass per nest (Table 2, Fig. 1B), that is, larger females produced more and larger eggs. Therefore, total clutch mass (the product of egg number and average egg mass) was positively correlated with female size (Table 2). Heavier eggs produced heavier hatchlings (Table 2, Fig. 2A). To test for the existence of an asymptotic egg mass, clutch size, or total clutch mass, I tested the goodness of fit of a second order polynomial to the untransformed data of each of the three variables versus female size (Sokal and Rohlf, 1995). Only the linear component explained the variation significantly. Therefore, there was no indication of an asymptotic value for any of these three variables as female size increases. The same analysis was performed to assess whether egg size reached a plateau as clutch size increased, and the result was also significant only for the linear component.

I failed to detect a trade-off between egg size and number. In the multiple regression analysis of clutch size against female size and egg size,

the resulting regression of the number of eggs on egg mass, holding female size constant, was not significant (Partial Reg. Coeff. = 0.39; $P = 0.61$). Likewise, residuals of the regression of clutch size on female size and of egg mass on female size were not associated (Reg. Coeff. = 0.0008, $F = 0.0007$, $P = 0.98$).

Constant incubation temperatures had a significant effect on hatchling size. The MANCOVA included hatchling weight, length, and width as response variables and incubation temperature, egg mass, and sex as explanatory variables (Table 3). All two-way and three-way interactions were nonsignificant and therefore excluded from the model. The results showed that sex and initial egg size had no effect on hatchling size (Table 3). The model was thus reduced to a one-way ANOVA test that showed that there were significant differences in hatchling mass ($F = 13.0$, $df = 3$, $P < 0.0001$) and width ($F = 8.86$, $df = 3$, $P < 0.0001$) among temperatures but not in hatchling length ($F = 2.04$, $df = 3$, $P = 0.12$). A posteriori multiple comparisons using Tukey-Kramer HSD test with a experimentwise $\alpha = 0.05$ (Sokal and Rohlf, 1995) revealed that hatchlings from 30.5°C were heavier than all the rest and wider than those from 32.5°C and 33.5°C.

TABLE 2. The relationship between female size, nest characteristics, and reproductive variables of *Podocnemis expansa* nesting in Colombian Amazonia. Reg.II = Regression Model II. Corr. = Correlation. RMA = Reduced Major Axis. MA = Major Axis. β = slope.

Variable 1	Variable 2	Analysis	β	r	P	N
Female size	Clutch size	Reg.II RMA	0.18		0.0001	64
Clutch size	Nest depth	Correlation		0.31816	0.0001	142
Female size	Nest depth	Reg.II RMA	0.52		0.0001	60
Clutch size	Egg size	Correlation		0.26740	0.0139	84
Female size	Egg size	Reg.II RMA	1.03		0.0001	87
Female size	Total clutch mass	Reg.II RMA	0.004		0.001	64
Avg. egg size	Avg. hatchling size	Reg.II MA	0.40664	0.87769	0.0001	14

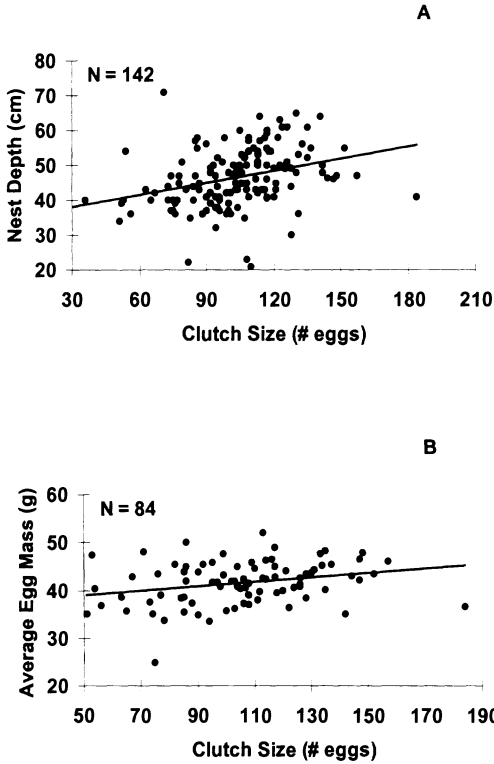


FIG. 1. Relationship between (A) clutch size and depth of the nest; (B) clutch size and average egg size per nest in *Podocnemis expansa* from the Caquetá River in Colombia.

Hatchlings from 34.5°C were also wider than those from 32.5°C. At two months of age, there were no significant differences among temperature treatments in hatchling mass, length, or width.

Smaller individuals at hatching grew more than large ones during their first two months of life. The MANCOVA included length growth and width growth as response variables and width and length at hatching, initial egg mass, incubation temperature, and sex as explanatory variables (Table 3). All two-way, three-way interactions, and the effects of incubation temperature, initial egg size, and sex were nonsignificant and excluded from the model. Size of individuals at hatching negatively affected width and length growth in all but one case (length at hatching was positively related to width growth).

Survival of hatchlings during their first two months of life was positively related to their size at emergence both in the lab and in the field (Wilks' $\Lambda = 0.15$ and 0.93 respectively, $P < 0.001$). The MANCOVA included hatchling mass, length, and width as dependent variables and survival (alive/dead), initial egg mass, and

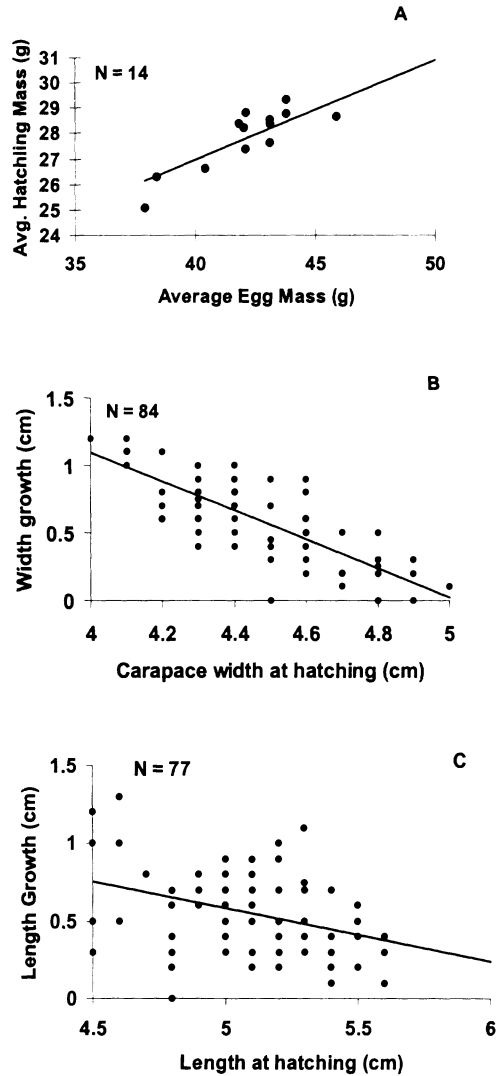


FIG. 2. Relationship between (A) average egg size and average hatchling size; (B) carapace width at hatching and early growth of laboratory individuals; (C) carapace length at hatching and early growth of laboratory individuals of *Podocnemis expansa*.

incubation temperature as explanatory variables (Table 3). For the laboratory, results of the MANCOVA indicated that initial egg mass did not have a significant effect and was therefore ignored. On the other hand, constant incubation temperature did have a significant effect in this relationship, but the interaction term was not significant, indicating that the effect was homogeneous for both groups (alive and dead). Lab hatchlings that survived were significantly heavier and wider (although shorter) than dead hatchlings (Table 3). In contrast, all two-way and three-way interaction terms were significant in

TABLE 3. Results from MANCOVA testing the relationship between incubation temperature and hatchling morphology and the effect of size at hatching on growth and survival in *Podocnemis expansa*.

Response variables	Explanatory variables	Wilks' Λ	F	df		P
				Num, Den		
Mass at hatching	Constant temperature	0.70	3.63	6, 114		0.0025
Length at hatching	Initial egg size	0.94	1.76	2, 56		0.18
Width at hatching	Hatchling Sex	0.99	0.17	2, 49		0.84
Width-growth	Length at hatching	0.51	41.6	1, 43		0.0001
Length-growth	Width at hatching	0.78	12.3	1, 43		0.0001
	Initial egg size	0.98	0.85	1, 38		0.36
	Constant temperature	0.93	0.91	3, 38		0.34
	Sex	1.0	0.05	1, 38		0.83
Mass at hatching	Survival in the field	0.97	9.3	2, 596		0.0001
Length at hatching	Initial egg size	0.95	14.7	2, 596		0.0001
Width at hatching	Mean nest temperature	0.95	14.5	2, 596		0.0001
	S * IES	0.97	9.2	2, 596		0.0001
	S * MNT	0.97	9.2	2, 596		0.0001
	IES * MNT	0.95	14.5	2, 596		0.0001
	S * IES * MNT	0.97	9.1	2, 596		0.0001
Mass at hatching	Survival in the lab	0.097	259.1	2, 56		0.0001
Length at hatching	Initial egg size	0.97	0.89	2, 55		0.42
Width at hatching	Constant temperature	0.76	2.73	6, 112		0.016

the MANCOVA for the field individuals. However, the biological relationship remained unchanged: surviving hatchlings in the field were heavier, longer, and wider at emergence than dead hatchlings (Table 3).

DISCUSSION

Female size and nest depth.—The results obtained in this study reveal that larger females lay larger clutches that are buried deeper than those from smaller females, as suggested by Ramírez (1956). This is in direct contrast with observations from *Chelonia mydas*, another large-bodied turtle species, where nest depth was found to be independent of female size (Hays et al., 1993). Female size differences in a population sample may not necessarily reflect age differences. Females of equal age could have experienced different juvenile growth trajectories (perhaps related to resource availability) and thus show size differences (Congdon and Gibbons, 1990). However, for a given individual increases in size are coupled with increases in age (Congdon and Gibbons, 1990). Therefore, because indeterminate growth has been observed directly in *P. expansa* (Ojasti, 1971), females should dig deeper nests with age as they continue to grow after maturity.

Profiles of temperatures at different depths vary considerably. A study of this same population showed that soil and nest temperatures fluctuate closer to the surface more than at greater depths, and mean temperatures decreased between 5 cm and 65 cm (Valenzuela, 1999), an ecologically relevant range of depths

since it overlaps with those found in natural nests (this study). Nest depth can affect important biological parameters in turtles and other oviparous reptiles, including CO₂ concentration during egg development (Christain and Lawrence, 1991), clutch survivorship (Mortimer, 1990), anaerobic metabolism related to hatchling emergence (Dial, 1987), and hatchling health (Chen and Cheng, 1995) among others. Furthermore, nest depth can affect sex ratio in *P. expansa* (Valenzuela, 1999) and other TSD species (Georges, 1989). The proportion of females increases with incubation temperature in *P. expansa* (Alho et al., 1985; Lance et al., 1994; Valenzuela et al., 1997) such that there may be a potential for shallow nests to produce more females, whereas deeper nests may produce more males. Given the relationship found here between female size and nest depth, larger females in the population may produce more males than smaller ones, and a given female may produce more daughters early in her reproductive life than when she is older if her size increases after maturity. The offspring sex ratio might be balanced over the lifetime of an individual female. However, changes in the population sex ratio could occur if the largest females are harvested for markets, as has happened for over a century (Hildebrand et al., 1997, and references therein).

Tests of optimality theory.—Optimal propagule size models state that the optimal egg size occurs at a point where a further increase in size will decrease fitness by reducing the total number of eggs, without compensating benefits of

increasing hatchling survival (Smith and Fretwell, 1974; Brockelman, 1975). Negligible variation in egg sizes across all female and clutch sizes within populations has been interpreted as evidence of the existence of an optimal egg size (Congdon and Gibbons, 1987). Such independence has been reported for a number of turtle species including *Apalone ferox* (Iverson and Moler, 1997), *Caretta caretta* (Hays and Speakman, 1991), and *Chelonia mydas* (Bjorndal and Carr, 1989). The data presented here showed a positive relationship between clutch size and egg size, suggesting that *P. expansa* does not conform to the optimal propagule size models. Examples of other turtle species showing a similar pattern are *Malaclemys terrapin* (Roosenburg and Dunham, 1997), *Emydoidea blandingii* (Rowe, 1992), *Trachemys scripta*, *Chrysemys picta*, and *Deirochelys reticularia* (Congdon et al., 1983; Congdon and Gibbons, 1987). The positive relationship found in those studies was explained by the authors as a constraint of the pelvic aperture on egg size in the cases of *C. picta* and *D. reticularia* but not in *T. scripta* (Congdon and Gibbons, 1987) or *M. terrapin* (Roosenburg and Dunham, 1997). Congdon and Gibbons (1987) argued that small females were limited to producing offspring of suboptimal size and fitness (although changes in egg length were not investigated) and that, as the females grow, the pelvic canal increases in diameter allowing larger (more optimal) eggs to be produced. For this to be true, an optimal egg size must exist in those species, which would be identified by a plateau of egg size as female size increases. A positive relationship without a plateau does not provide evidence of an optimal egg size even if one actually exists. Egg mass in *P. expansa* did not plateau as female or clutch size reached the largest values. Likewise, clutch size and total clutch mass did not reach a plateau as female size increased. The mean straight carapace length of adult females at the study area is 70 cm (50–82 cm; Hildebrand et al., 1997). The maximum recorded carapace length is 89 cm (Pritchard and Trebbau, 1984). Thus, the sizes in the population studied are representative of those attained by this species. The results suggest that as adult *P. expansa* females grow larger and hold more total energy, they devote more energy (in absolute terms) to reproduction, as indicated by the increase in total clutch mass with body size. Further, the data suggest that larger females allocate this energy to the production of both more eggs and larger eggs. These results show no evidence of the existence of an optimal egg size or clutch size nor of a trade-off between clutch size and egg mass.

Rowe (1992) suggested that the lack of a trade-off could only be found after removing the

effect of female size, if the relationship between egg and clutch size remains positive. I performed a multiple regression of clutch size against female and egg size, as well as residual analysis, and the results were the same, namely, clutch size and egg size were not associated significantly after removing the effect of female size. The variables were independent of each other, and it should be noted that the trend in both analyses was positive. A trade-off would cause the relationship between these two variables to be negative after removing the effect of female size as in the case of *Chrysemys picta* (Rowe, 1994) and *Malaclemys terrapin* (Roosenburg and Dunham, 1997). A similar result to the one found in the present study for *P. expansa* was reported for *Chelonia mydas* (Hays et al., 1993).

The number and size of eggs a female lays also may be affected by resources accumulated between reproductive bouts, such that variation in seasonal resources would cause a female to produce larger or smaller clutches than expected solely by her size (Fraser, 1980; Etchberger and Ehrhart, 1987; Seigel and Ford, 1991; Dodd, 1997). But even in a year of abundance, a well-provisioned female will still be limited to producing eggs of a size that can pass through her pelvic aperture and a number that she can fit in her body cavity. Females could also use the extra energy accumulated in a plentiful year by laying more than one clutch per season, although *P. expansa* females lay only one clutch per year (Pritchard and Trebbau, 1984).

The results obtained from the artificial incubation experiments indicate that constant temperatures affect hatchling size in this species regardless of sex or initial egg size. Significantly heavier and wider individuals were produced at lower than at higher temperatures (Fig. 3), consistent with observations from other reptile species (Gutzke et al., 1987; Van-Damme et al., 1992; Spotila et al., 1994; Booth, 1999; Florentino and Xiang, 2000). In some reptiles, hatchling size correlates positively with incubation temperature (e.g., Janzen, 1993), whereas in others the relationship is more complex (Cagle et al., 1993; Packard et al., 1993; Bobyn and Brooks, 1994; Allstead and Lang, 1995) or nonexistent (Griffiths and De Wijer, 1994).

Optimality models assume that a larger hatchling is more fit compared to smaller ones because of advantages in survival or growth (see Smith and Fretwell, 1974:figs. 1–2; Brockelman, 1975), and the “bigger is better” hypothesis states that directional selection would favor larger offspring if body size is positively correlated with traits that are related to fitness (Congdon et al., 1999). Although larger eggs produced larger hatchlings in this study (Fig. 3A), I did not find evidence of an advantage in

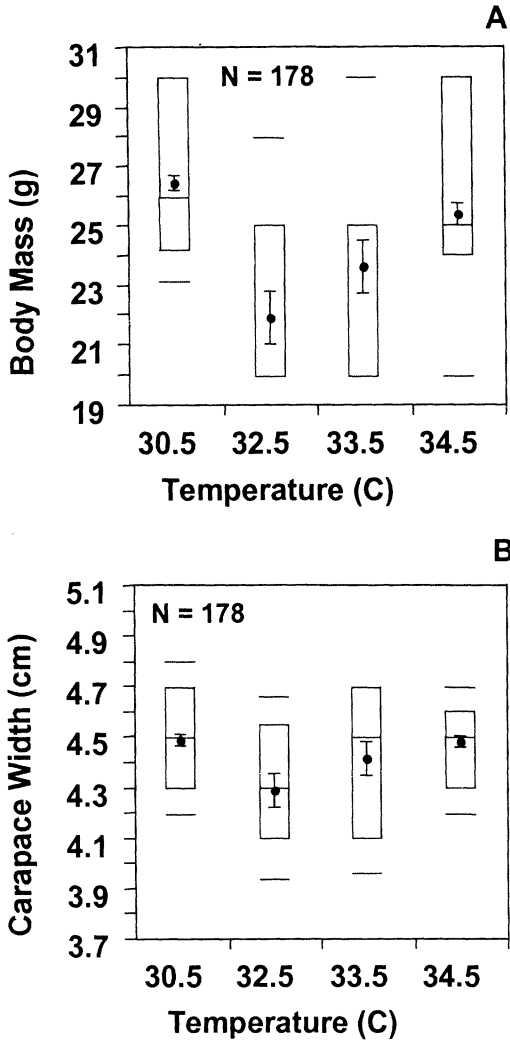


FIG. 3. ANOVA of (A) hatchling mass by constant incubation temperature, and (B) hatchling straight-line carapace width by constant incubation temperature of Colombian *Podocnemis expansa*. The graphs include the mean (dots), error bars, quartile boxes, and range of values for each group.

growth by the larger individuals but by the smaller ones at early stages of life, at least under unlimited food conditions (Fig. 2B–C; Table 3). The effects of incubation temperature, initial egg size, and sex in this case were not significant (Table 3). On the contrary, the short-term survival of hatchlings was positively related to their size at emergence (Table 3). In this case, initial egg size did not have an effect in the laboratory but incubation temperature did, although this effect was homogeneous for both groups (alive and dead). In contrast, the effect of initial egg size and mean nest temperature (plus all interaction terms) were significant in the field, but

the biological signal remained unaltered, that is, bigger hatchlings exhibited higher survival. The patterns of survival and growth found here are consistent with observations of *Chelydra serpentina* and *Sceloporus occidentalis* where larger hatchlings survived better but grew less than smaller hatchlings (Sinervo, 1990; Bohnen and Brooks, 1994). Greater survival of larger hatchlings compared to smaller ones has been reported for several other turtle and reptile species (e.g., Ferguson and Bohlen, 1978; Fox, 1978; Marion et al., 1979; Swingland and Coe, 1979; Ferguson et al., 1982; Ferguson and Fox, 1984; but see Sorci and Colbert, 1999). Contrary to my findings, greater growth of larger hatchlings has been reported for several other reptile species (e.g., Luiselli et al., 1996; Olsson et al., 1996; Keller et al., 1997).

I suggest that *P. expansa* females might improve their fitness by increasing the size of their eggs, and this fitness increase is manifested in greater offspring survivorship, not in increased growth rates, at least early in life. It is worth noting that the difference between the smallest and largest egg in this study was slightly more than twofold (25 to 52 grams), whereas the difference between the smallest and largest clutch was almost fourfold (50–184 eggs). Similar observations have been reported for *Malaclemys terrapin* (Roosenburg and Dunham, 1997). This smaller variation in egg size compared to egg number is expected if selection acts on egg size within populations (Lloyd, 1987), and my results revealed a fitness advantage of larger eggs via the higher survival exhibited by larger hatchlings, which is consistent with that hypothesis. More extensive studies are necessary to test this hypothesis in an evolutionary context.

Estimates of body size from trackways.—Previous studies in which females were measured directly found a positive relationship between female size and clutch size in *P. expansa* in Brazil (Alho and Pádua, 1982) and in the Caquetá River in Colombia (Hildebrand et al., 1997). This latter survey was carried out on the same population of turtles used in the present study. No work so far has included an analysis of clutch and egg size nor of nest depth in this species. I also found a positive association between estimated female size and clutch size. The detection of the same pattern suggests that trackway data provided a sufficient measure of female size, as has been demonstrated for *Podocnemis unifilis* (T. Escalona, unpubl. data). However, the associations found by Alho and Pádua (1982) and Hildebrand et al. (1997) are stronger than the association detected using trackways data. This could be a result of increased measurement error of the trackway data derived from several

factors, including variation in gate and modifications of the tracks by rain, wind, and other climatic factors. Taking multiple measurements along the trackway and using the average may improve this index, although measurements were taken where width values were the same at 3–4 points along the trackway. Finally, there are two additional merits of the method used in this study. First, it was possible to capture signals present in the data that showed important biological patterns without disturbing females in their nesting behavior. This is particularly important because *P. expansa* is endangered and perturbations can cause females to abort digging the nest hole or covering the eggs already deposited (Hildebrand et al., 1997), an observation that has elicited the requirement of the local indigenous authorities to avoid handling females. Second, compared to direct measurements of female size, data taken from trackways results in larger sample sizes from multiple beaches while requiring smaller field crews.

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A New Anole from the Northern Slope of the Sierra Maestra in Eastern Cuba (Squamata: Iguanidae)

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ABSTRACT.—A new species of anole is described from a region of wet limestone forest in the province of Santiago de Cuba in eastern Cuba. It is sympatric with its close relative *Anolis isolepis* and differs from that taxon in scalation and coloration. Variation in the two subspecies of *A. isolepis* is reconsidered, and they are here regarded as separate species. These three small species with short limbs, a relatively flat head, striate head scales, and green coloration in the light phase are placed in the *isolepis* group of the *carolinensis* series. At least 14 and as many as 20 species of *Anolis* are sympatric in this region of eastern Cuba.

RESUMEN.—Se describe una nueva especie de *Anolis* de los Bosques húmedos de “diente perro” de la provincia de Santiago de Cuba en la región oriental. Esta especie es simpátrida con la formaafin *Anolis isolepis*, diferenciándose de este taxón en escamación y coloración. Se reconsidera la variación entre las dos subspecies de *A. isolepis* considerandon a ambas formas como especies diferentes. Estas tres especies de miembros cortos, de cabeza relativamente plana, con sus escamas estriadas, y coloración verdosa en la fase clara, son consideradas bajo el grupo *isolepis* de la serie *carolinensis*. No menos de 14, y posiblemente 20 especies de *Anolis* son simpátridas en la región oriental de Cuba.

Anolis isolepis is a small, short-limbed, greenish Cuban species of anole placed in the *carolinensis* series along with other mostly green- or blue-colored species (Williams, 1976; Burnell and Hedges, 1990). It was described by Cope (1861) from material sent to him by the botanist

Charles Wright (Underwood, 1905) from Monte Verde, Yateras Municipio, Guantánamo Province, Cuba. Since its original description, it has been encountered infrequently and is considered to be rare (Gundlach, 1880; Barbour and Ramsden, 1919; Ruibal, 1964; Schwartz and Henderson, 1991). Garrido (1985) reported on some new material and described a subspecies, *Anolis iso-*

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