

Clutch and egg allometry of the turtle *Mauremys leprosa* (Chelonia: Geoemydidae) from a polluted peri-urban river in west-central Morocco

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We examined the relationships of clutch size (CS) and egg size to female body size (straight-line carapace length, CL) in a population of the turtle *Mauremys leprosa* from a polluted segment of oued (river) Tensift in arid west-central Morocco. Twenty-eight adult females were collected in May–July, 2009 and all were gravid. Each was weighed, measured, humanely euthanized and then dissected. Oviductal shelled eggs were removed, weighed (egg mass, EM) and measured for length (EL) and width (EW). Clutch mass (CM) was the sum of EM for a clutch. Pelvic aperture width (PAW) was measured at the widest point between the ilia bones through which eggs must pass at oviposition. The smallest gravid female had a CL of 124.0 mm. Mean CS was relatively large (9.7 ± 2.0 eggs, range: 3–13) and may reflect high productivity associated with polluted (eutrophic) waters. Regression analyses were conducted using log-transformed data. CM increased isometrically with maternal body size. CS, EW and EM were all significantly hypoallometric in their relationship with CL. EL did not change significantly with increases in CL. EW increased at a hypoallometric rate with increasing CL but was unconstrained by PAW since the widest egg was smaller than the narrowest PAW measurement when excluding the three smallest females. Smaller females may have EW constrained by PAW. As females increase in size they increase both clutch size and egg width in contradiction to predictions of optimal egg size theory.

Key words: clutch size, constraint, Morocco, optimal egg size, turtle

INTRODUCTION

Organisms must apportion harvested resources among the competing requirements for growth, maintenance, reproduction and storage (Congdon et al., 1982). Since acquisition and processing of resources is finite during a given period of time (e.g. the activity season or lifetime of an individual), allocation is a delicate balance between survival and reproduction. If resource availability allows for increased reproductive output in oviparous species, they can produce larger eggs, more eggs per clutch, multiple clutches or a combination of more and larger eggs. Producing more eggs per clutch can only occur if physical accommodation is possible, usually through increased maternal body size (volume). Optimal egg size theory predicts that natural selection operates to balance reproductive output to optimize egg size (Smith and Fretwell, 1974; Brockelman, 1975) and presumably hatchling viability, thus increasing female fitness. Eggs produced below the optimal size would be expected to produce hatchlings with lower viability. If a species has evolved an optimum egg size, fitness of large females is expected to increase by producing more eggs of that size rather than producing an increased number

of smaller eggs or fewer larger eggs. Optimization thus occurs at the point where fitness gained by investing in larger eggs is balanced with fitness reductions associated with production of fewer eggs (Congdon and Gibbons, 1985). However, optimal egg size is constrained in some turtle species by pelvic aperture width or other anatomical constraints imposed by the turtle body plan (see review in Ryan and Lindeman, 2007).

In this study, egg and clutch allometry were quantified, relative to body size, in a population of the turtle *Mauremys leprosa* from a polluted segment of oued (river) Tensift in west-central Morocco. The study had three objectives. First, we examined the relationships between female size measured as carapace length (CL) and the following variables: clutch size (CS), clutch mass (CM), egg width (EW), egg length (EL) and egg mass (EM). Second, we investigated the possibility that egg size was optimized in this species and not constrained by pelvic aperture width (PAW) as has been shown in other small-bodied turtle species (Congdon and Gibbons, 1987). Third, our data were compared and contrasted with other studies in both polluted and unpolluted waters. The species has a broad western circum-Mediterranean distribution across a wide variety of habitats (Lovich et al., 2010) from the

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northern margin of the Sahara to the French Pyrenees and from the Atlantic coasts to Tripolitania in Libya (Schleich et al., 1996; Bour and Maran, 1999). Consequently, we hypothesized that turtles living in eutrophic habitats (as found in many polluted environments) with higher food availability produce more eggs than those in less productive habitats due to the potential for increased growth rates and body sizes (Ernst and McDonald, 1989; Germano, 2010).

MATERIALS AND METHODS

Study area

The study area is located in a segment of oued Tensift west of Marrakech, Morocco (32°N, 7°W and 380 m a.s.l.) in a peri-urban zone within the arid Haouz plain. This reach of the river is heavily polluted due to the proximity of a garbage dump and direct discharges of raw domestic and industrial wastewaters. Oued Tensift has its source in the nearby High Atlas Mountains. The river is subject to marked hydrological fluctuations with two peak flows: one in autumn/winter and a second in the spring. The annual mean rainfall in the area is 242 mm, and the annual mean temperature is 20 °C, with minimal (January) and maximal (July) monthly means of 4.5 and 38.9 °C, respectively. The adjacent marsh vegetation is dominated by *Phragmites* sp., *Juncus* sp. and *Typha* sp. The river bed is occupied by ca. 10 halophilous shrub species belonging to six different families (Hammada et al., 2004) due to high levels of soil salinity. The river showed high levels of eutrophication due to discharges of sewage and waste. Turtles were very abundant in the area.

Except for short periods in the winter when intermittent floods flush the channel, the river is shallow (0.15–1.00 m). The water is highly turbid (Secchi depth <10 cm) and the bottom of the river is usually covered by a mat of saprobic material composed of decaying organic substrate supporting an algae-fungi complex. The invertebrate fauna generally consists of a few species of aquatic insects, mostly chironomids. Except for occasional observations of some amphibians (Green Toad, *Pseudepidalea viridis* and Mauritanian Toad, *Amietophrynus mauritanicus*), *M. leprosa* appeared to be the most common aquatic vertebrate in this polluted segment of river. However, wading birds such as White Storks, *Ciconia ciconia*, and Cattle Egrets, *Bubulcus ibis*, were frequently observed.

Methods

The local abundance of *M. leprosa* and the low water depth of oued Tensift at the study site facilitated hand capture of turtles. During the 2009 breeding season, from May through July, adult turtles (CL>110 mm) were captured and then transported to the laboratory. Females were weighed (± 0.1 g), measured for straight-line carapace length (± 0.1 mm), and humanely euthanized (following administration of deep anesthesia with diethyl ether) prior to dissection.

The plastron was removed by sawing the bridges of the carapace and cutting the muscles beneath. CS was determined based on the number of shelled oviductal eggs. Ovaries were not examined to determine the number of

clutches produced that season so our results may include both first and subsequent clutches. Eggs were removed, numbered, weighed to the nearest 0.1 g and EL and EW were measured to the nearest 0.1 mm. We used the mean of egg measurements for each clutch in our analyses to control for maternal effects. CM was the sum of individual egg mass (EM) within a clutch. Relative clutch mass (RCM) was calculated as CM divided by the postpartum body mass (body mass without eggs) of the female. Finally PAW for each female was measured directly at the widest point between the ilia using a digital caliper (to the nearest 0.1 mm). All the specimens examined are preserved and maintained in the collection at the Natural History Museum of Marrakech, Cadi Ayyad University, Morocco.

Relationships among the various clutch and egg characteristics, CL and PAW were examined by linear regression after \log_{10} transformation to improve linearity, reduce or eliminate heteroscedasticity and to facilitate comparisons with other studies (King, 2000). Preliminary regression analyses demonstrated that the three smallest females (CL=124.0 mm, CS=3; CL=142.0 mm, CS=4; and CL=156.5 mm, CS=5) caused skewed normal probability plots even after log transformation. As a result, they were removed from all regression analyses but are included in statistical summaries of variables and for reference in Fig. 1 and 2. Following Ryan and Lindeman (2007), linear regression analysis was used to identify isometric versus allometric (hypoallometric or hyperallometric) relationships. For volumetric measures, such as CS or egg mass (EM), we hypothesized an isometric relationship with a slope of 3 when regressed on CL. For comparison of linear measurements like EW and EL against CL, an isometric relationship with a slope of 1 was hypothesized. Significant results with 95% confidence intervals that bracketed the expected slope value under isometry were considered to be support for that hypothesized relationship. Confidence intervals that were below expected slope values were hypoallometric (increasing at a rate less than expected under isometry) while values above expected slope values were hyperallometric (increasing at a rate greater than expected under isometry).

To determine the relationships of PAW and EW with CL, the method of Congdon and Gibbons (1987) and van Loben Sels et al. (1997) was used by employing analysis of covariance to test for homogeneity of slopes. Homogeneity of slopes (CL vs. PAW=CL vs. EW) can suggest the existence of a morphological constraint on EW. Heterogeneity of slopes suggests that egg size is optimized if EW does not increase with CL. Coefficients of variation for EW and CS were compared since CS is expected to vary more than EW under optimal egg size theory. Again, the three smallest females were excluded from the analysis so the results should be interpreted for larger females from our population.

Means are reported along with their standard deviations. All tests were evaluated at $\alpha=0.05$. Statistical tests were carried out by using SPSS 10.0 and SYSTAT 13 software.

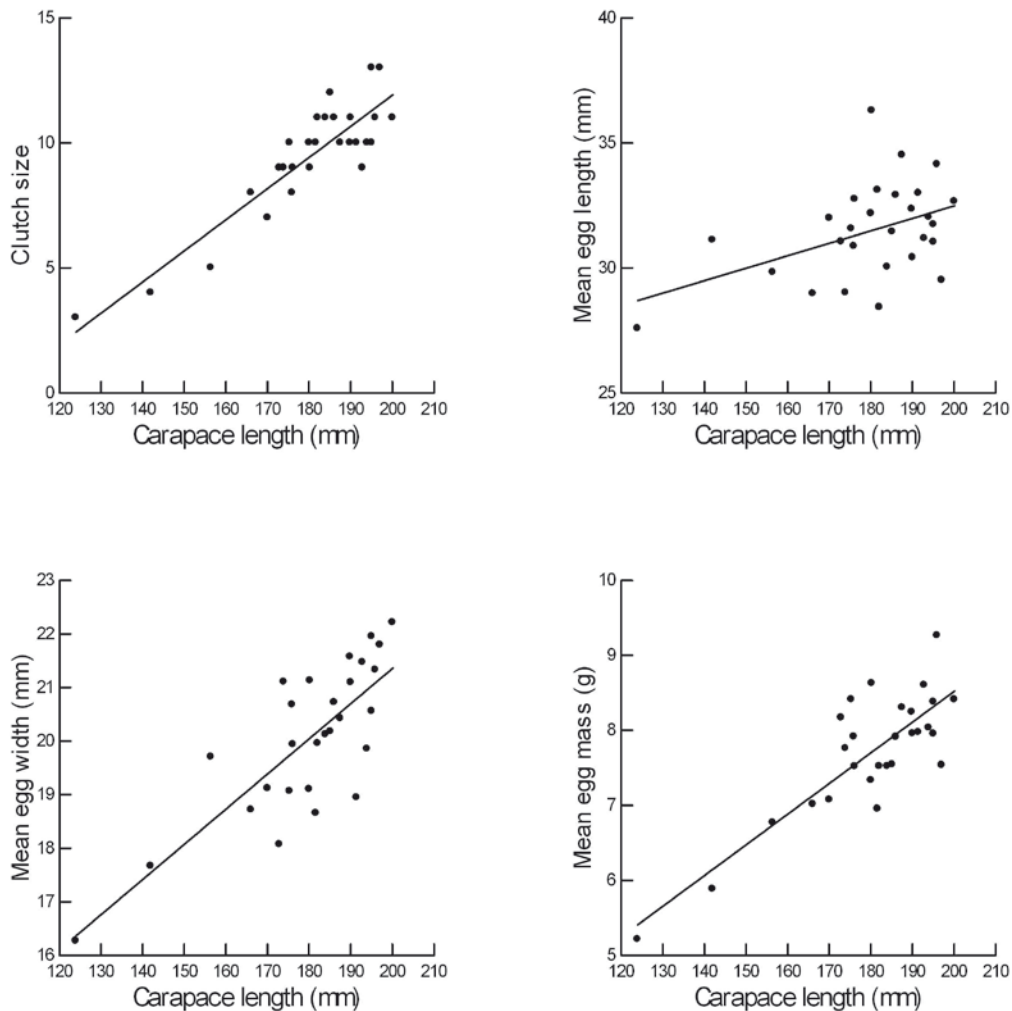


Fig. 1. The relationship between clutch size and other clutch/egg characteristics in *Mauremys leprosa* from oued Tensift, Morocco. Linear regression smoothers are fitted to the data for reference only since the three smallest gravid females were outliers that challenged the assumption of normality.

RESULTS

All 28 of the females collected and examined were gravid with shelled eggs in their oviducts. Mean female CL was 180.1 ± 17.0 mm (range: 124.0–200.1 mm). Mean body mass was 979.8 ± 198.3 g (range: 550.0–1,295.0 g). CS varied from 3 to 13 eggs with a mean of 9.7 ± 2.0 . Mean egg mass was 7.5 ± 1.3 g (range: 3.4–9.3 g). Mean CM was 74.0 ± 21.7 g (range 15.6–108.9 g). Mean RCM was $7.4 \pm 1.5\%$ (range: 2.3–9.2%). Despite the variation in RCM, the log-log relationship with CL was not significantly different from zero ($r=0.04$, $P=0.85$). Mean EL and EW were 31.5 ± 1.9 mm (range: 27.6–36.3 mm) and 20.0 ± 1.41 mm (range: 16.3–22.2 mm), respectively. The average PAW (mm) was 27.8 ± 3.2 (range: 19.3–32.8 mm). CS, CM, EW and EM were all significantly correlated with female CL ($P < 0.05$ in all cases, Table 1). A significant isometric relationship existed between CM and maternal CL (Fig. 1). CS, EW and EM increased in a significantly hypoallometric fashion with maternal CL (Fig. 1) in contrast to our predictions of isometry. EL was not significantly related to CL (Table 1).

Comparing the slopes of the two log-transformed regression equations relating both PAW and EW to the covariate CL (Fig. 2) using ANCOVA, after removing the three smallest females, we rejected the null hypothesis of homogeneity of slopes as shown by a significant interaction term (Table 1). PAW increased at a hyperallometric rate relative to CL (Table 1). The coefficient of variation for the log of CS was 0.058 while that for the log of EW was 0.019.

DISCUSSION

Data on the reproductive ecology of *M. leprosa* are relatively scarce, especially within Morocco. The first work on reproductive biology of this species dealt with the gonadic cycle of populations in Algeria (Combescot, 1954). Many years later, several studies were published for Iberian populations (Spain: Perez et al., 1979; Andreu and Villamor, 1989 and da Silva, 1995). In Morocco, apart from works on aspects of population ecology (Meek, 1987) and more recently on geographic variation of sexual dimorphism (Lovich et al., 2010), there are few studies on the ecology and life history traits of this species.

Table 1. Analysis of log-log linear regressions, between carapace length (CL), various egg characteristics (clutch mass=CM, clutch size=CS, mean egg length=EL, mean egg width=EW, and mean egg mass=EM) and pelvic aperture width (PAW) in *Mauremys leprosa* from oued Tensift, Morocco. Regression model parameters are given with correlation coefficients (r), standard errors (SE) and confidence intervals (c.i.). The three smallest females in the sample were excluded from the analyses to meet the assumption of normality. Therefore these regressions only apply to larger females.

Reproductive Parameters	r	P	Expected slope Under isometry	Slope	SE	95% c.i.	Result	y-intercept
log CM	0.79	<0.001	3	2.73	0.44	2.30–3.17	Isometry	-4.30
log CS	0.71	<0.001	3	2.03	0.42	1.61–2.45	hypoallometry	-3.60
log mean EL	0.23	0.271	1	0.26	0.23	0.03–0.48	hypoallometry	0.92
log mean EW	0.66	<0.001	1	0.74	0.18	0.56–0.91	hypoallometry	-0.36
log mean EM	0.51	0.009	3	0.71	0.25	0.46–0.95	hypoallometry	-0.701
log PAW	0.84	<0.001	1	1.43	0.19	1.24–1.62	hyperallometry	-1.79

Body sizes for females at our study site were similar to those in a polluted, eutrophic habitat in Badajoz, southwest Spain (Table 3). The size of the smallest egg-bearing female in oued Tensift was 124.0 mm CL which is smaller than the size at sexual maturity found in either Algeria (130 mm CL, Combescot, 1954) or Spain (Doñana, 140–150 mm CL; and Badajoz, 153.1–210.1 mm CL, da Silva, 1995). The small size at maturity we observed may be a result of rapid growth facilitated by eutrophic conditions. Ernst and McDonald (1989) and Germano (2010) found that turtles in eutrophic conditions grew faster and achieved larger body sizes than those in less productive habitats. It is possible that the productive conditions at our study site allow for earlier maturity of females relative to less productive sites. Local variation in the size and age of maturity is well-documented in turtles (Gibbons and Lovich, 1990), including *M. leprosa* in Morocco (Lovich et al., 2010).

Mean clutch size of our population was similar to values reported (Table 3) from eutrophic habitats in Badajoz, Spain (da Silva, 1995). In contrast, lower clutch sizes were found in unpolluted habitats in Algeria and other populations in Spain. The difference was attributed to the eutrophic nature of the habitat in Badajoz, Spain and could also explain the high clutch sizes we observed in the polluted habitat of oued Tensift. Higher clutch sizes in turtles from polluted (eutrophic) habitats may be related to the attainment of larger adult body sizes, and thus increased volume for egg storage, relative to less productive habitats. Gibbons et al. (1982) documented significant local variation in clutch size of turtles occupying habitats with different conditions.

In oued Tensift, clutch size and egg size were positively correlated with female CL. Similar results were observed in southwestern Spain (da Silva, 1995). This pattern has been observed in other turtle species (see review in Ryan and Lindeman, 2007). Log-log regression analyses showed that CM increased isometrically to carapace length with a slope of 3, indicating that as body size increases abdominal volume available for egg storage increases at a similar rate. CS, EW and EM were

hypoallometric to CL, suggesting that these increased much more slowly than expected based on increases in body size. EL was essentially invariant to CL since it is less likely than EW to be affected by morphological constraints.

No evidence of a morphological constraint from pelvic aperture size on EW was found since the widest egg was still smaller than the narrowest PAW observed in our sample when excluding the three smallest females. However, inspection of Fig. 2 suggests the possibility of a constraint in the smallest turtles. In fact, PAW increases at a hyperallometric rate relative to CL (Table 1) and this allows egg width to increase significantly with CL at a

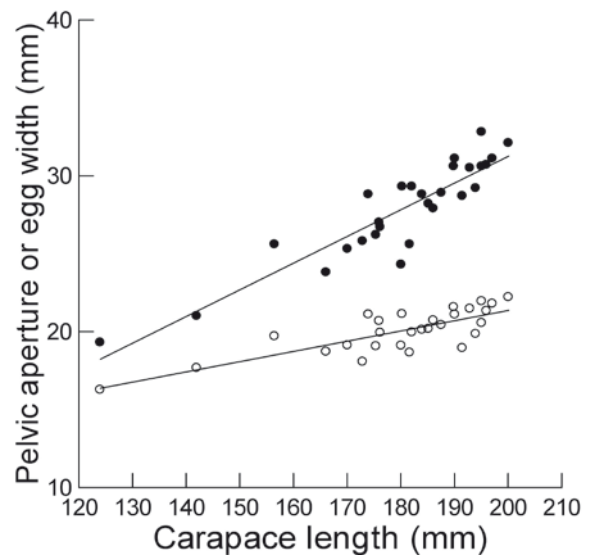


Fig. 2. Relationship between carapace length and mean egg width of each clutch (hollow circles) and pelvic aperture width (solid circles) in *Mauremys leprosa* from oued Tensift, Morocco. Linear regression smoothing functions are shown. The three smallest gravid females were removed from statistical analysis of linear regressions (as discussed in the text) to meet the assumption of normality, but they are plotted here for reference.

Table 2. Analysis of covariance results comparing the slopes of the relationships between log carapace length (CL) and log mean egg width, and log CL and log pelvic aperture width. Treatment is the log of mean egg width for a clutch or the log of pelvic aperture width; log CL was the covariate.

Source	Sum-of-Squares	df	Mean-Square	F-ratio	P
Treatment	0.002	1	0.002	5.951	0.019
log CL	0.028	1	0.028	70.238	0.000
Treatment*log CL	0.003	1	0.003	7.235	0.010
Error	0.018	46	0.000		

lesser rate (Fig. 2). This is in contrast to the prediction that EW is optimized and thus relatively invariant compared to CS across a wide range of body sizes (Congdon and Gibbons, 1985). Instead, both CS and EW increase with CL. This pattern was reported previously for *M. leprosa* in Spain (da Silva, 1995) and 12 other turtle species (Ryan and Lindeman, 2007) including *Graptemys geographica*. In *M. leprosa* and *G. geographica*, larger females divide increased reproductive effort between producing both larger clutches and larger eggs, again, in contradiction to expectations under optimal egg size theory. Thus, egg width is neither constrained nor optimized. While larger females produce both more and larger eggs, RCM is essentially constant across body sizes and this is consistent with the finding that CM increases isometrically with CL as in *G. geographica* (Ryan and Lindeman, 2007), and indeed in most turtles (Iverson, 1992; Iverson et al., 1993).

If EW is not constrained by PAW, why does EW increase with increasing CL? Another morphological variable, not measured in this study, that presents a potential physical constraint to oviposition in turtles is the caudal gap formed between the posterior rim of the carapace and the plastron (Clark et al., 2001). It is possible that this anatomical feature constrains egg size in

M. leprosa from being optimized, especially in small females. However, our sample size encompassed the range of body sizes observed in populations of *M. leprosa* in central Morocco (Lovich et al., 2010), and neither we nor Ryan and Lindeman (2007) found evidence of a sudden leveling off of egg size in larger females as observed in larger female painted turtles (*Chrysemys picta*) in some populations (Rollinson and Brooks, 2008). It is also possible that there are physiological constraints associated with body size (Bowden et al., 2004) or differences in resource allocation to reproduction between smaller and larger females (Bowden et al., 2011).

We were unable to determine the relative clutch number produced by each female. Thus, it is possible that females sampled early in the season were producing their first clutch while females sampled later in the season were producing a second or third clutch (Bonin et al. 2006). Clutch frequency can have an effect on egg size. For example, in the 20 year reproductive history of a captive female turtle *Heosemys grandis*, first clutches had few large eggs while second clutches had more but smaller eggs (Goode and Ewert, 2006). We are not aware of this phenomenon in *M. leprosa* but it warrants additional study.

Table 3. A comparison of reproductive attributes of female *Mauremys leprosa* from various populations in Morocco, Spain and Algeria. All size measurements in mm except egg mass in grams. Carapace length=CL. Data from Keller (1998) include two subsamples from the same population. For additional information on body size at maturity see Lovich et al. (2010: Table 2).

Location	Variable					
	Smallest gravid female CL	Maximum female CL	Clutch size (range)	Mean egg length	Mean egg width	Mean egg mass
Tensift River, Morocco (Present study)	124.0	200.1	9.7 (3–13)	31.5	20.0	7.4
Algeria (Combescot, 1954)	130	-	4.8 (4–6)	-	-	-
Doñana, Spain (Andreu and Villamor, 1989 and Pérez et al., 1979 in da Silva, 1995)	140	-	5.3 (3–7) 5.8 (5–7)	35.5	22.4 21.3	-
Doñana, Spain (Keller, 1998)	137.3	218.0	6.9 (3–13) 6.2 (1–10)			
Badajoz, Spain (da Silva, 1995)	153.1	210.1	9.6 (4–13)	34.1	20.1	8.4

The reproductive strategy of our population of *M. leprosa* does not appear to require egg size optimization. Instead, the species divides increased investment of reproductive effort between producing both more and larger eggs as body size allows. The coefficients of variation we calculated for CS and EW suggest that the former varies more than the latter, in partial support of predictions from optimal egg size theory. What value might this strategy of increasing both CS and EW have in terms of female fitness? A possible explanation is phenotype-habitat matching as suggested by Rollinson and Brooks (2008). It could also be that there are nearly equal fitness advantages to larger clutches and larger eggs. Hence the optimal “strategy” could simply be to increase both parameters with size. Female body size may influence hatchling survival if larger females nest farther from water than smaller females, where predation risk is minimized (but see Congdon et al., 1983). Larger eggs might better provision hatchlings for the long trip back to water upon emergence (Janzen et al., 2000). If phenotype-habitat matching occurs in *M. leprosa*, this might be expected to cause egg size to covary with body size as observed in our study.

ACKNOWLEDGEMENTS

Research was carried out under permits issued to Mohamed Znari (Decision #115 HCEFLCD/DLCDPN/DPRN/CFF provided by the Haut Commissariat aux Eaux et Forêts et à la Lutte Contre la Désertification, Moroccan Waters and Forests Service) in Rabat. Special thanks to the Fulbright Program of the U.S. Department of State for facilitating our collaboration with grants to both Lovich and Znari. We are also indebted to Professor Lahcen Ameziane, the Dean of the Faculty of Sciences - Semlalia, Cadi Ayyad University, Marrakech, Morocco for providing support for our collaboration. Earlier versions of this manuscript benefitted from comments offered by R. Bruce Bury, John Iverson, and Peter Lindeman. The use of product names in this article does not constitute an endorsement by the U.S. Geological Survey.

REFERENCES

- Andreu, A., & Villamor, M. C. (1989). Calendario reproductivo y tamaño de la puesta en el galapagoleproso, *Mauremys leprosa* (Schweiger, 1812) en Doñana. *Doñana Acta Vertebrata* 16, 167–172.
- Bonin, F., Devaux, B. & Dupré, A. (2006). *Turtles of the World*. (Translated by Pritchard PCH). Baltimore: Johns Hopkins University Press.
- Bour R. & Maran J., (1999). Taxinomie de *Mauremys leprosa* (Schweiger, 1812) dans le sud du Maroc : la “tortue aux yeux bleus” (Reptilia, Chelonii, Geoemydidae). *Manouria* 2, 22–49.
- Bowden, R.M., Paitz, R.T. & Janzen, F.J. (2011). The ontogeny of postmaturation resource allocation in turtles. *Physiological and Biochemical Zoology* 84, 204–211.
- Bowden, R.M., Harms, H.K., Paitz, R.T., & Janzen, F.J. (2004). Does optimal egg size vary with demographic stage because of a physiological constraint? *Functional Ecology* 18, 522–529.
- Brockelman, W.Y. (1975). Competition and fitness of offspring, and optimal clutch size. *American Naturalist* 109, 677–699.
- Clark, P. J., Ewert, M.A., & Nelson, C.E. (2001). Physical apertures as constraints on egg size and shape in the common musk turtle, *Sternotherus odoratus*. *Functional Ecology* 15, 70–77.
- Combescot, C.H. (1954). Sexualité et cycle génitale de la tortue d’eau algérienne, *Emys leprosa* Schw. *Bull. Soc. Hist. Nat. Africa Nord* 45, 366–377.
- Congdon, J.D. & Gibbons, J.W. (1985). Egg components and reproductive characteristics of turtles: relationships to body size. *Herpetologica* 41, 194–205.
- Congdon, J.D. & Gibbons, J.W. (1987). Morphological constraint on egg size: a challenge to optimal egg size theory? *Proceedings of the National Academy of Sciences of the United States of America* 84, 4145–4147.
- Congdon, J.D., Dunham, A.E., & Tinkle, D.W. (1982). Energy budgets and life histories of reptiles. In *Biology of the Reptilia, Vol. 13*, 233–271. Gans C. (ed). New York: Academic Press.
- Congdon, J.D., Tinkle, D.W., Breitenbach, G.L., & van Loben Sels, R.C. (1983). Nesting ecology and hatching success in the turtle *Emydoidea blandingii*. *Herpetologica* 39, 417–429.
- da Silva E. (1995). Notes on clutch size and egg size of *Mauremys leprosa* from Spain. *Journal of Herpetology* 29, 484–485.
- Ernst, C.H. & McDonald, B.S., Jr. (1989). Preliminary report on enhanced growth and early maturity in a Maryland population of painted turtles, *Chrysemys picta*. *Bulletin of the Maryland Herpetological Society* 25, 135–142.
- Germano, D.J. (2010). Ecology of western pond turtles (*Actinemys marmorata*) at sewage-treatment facilities in the San Joaquin Valley, California. *Southwestern Naturalist* 55, 89–97.
- Gibbons, J.W. & Lovich, J.E. (1990). Sexual dimorphism in turtles with emphasis on the slider turtle (*Trachemys scripta*). *Herpetological Monographs* 4, 1–29.
- Gibbons, J.W., Greene, J.L., & Patterson, K.K. (1982). Variation in reproductive characteristics of aquatic turtles. *Copeia* 1982, 776–784.
- Goode, J.M. & Ewert, M.A. (2006). Reproductive trends in captive *Heosemys grandis* (Geoemydidae). *Chelonian Conservation and Biology* 5, 165–169.
- Hammada S., Dakki M., Ibn Tattou M., Ouyahya A. & Fennane M. (2004). Analyse de la biodiversité floristique des zones humides du Maroc. Flore rare, menacée et halophile. *Acta Botanica Malacitana* 29, 43–66.
- Iverson, J.B. (1992). Correlates of reproductive output in turtles (order Testudines). *Herpetological Monographs* 6, 25–42.
- Iverson, J.B., Balgooyen, C.P., Byrd, K.K., & Lyddan, K.K. (1993). Latitudinal variation in egg and clutch size in turtles. *Canadian Journal of Zoology* 71, 2448–2461.
- Janzen, F.J., Tucker, J.K., & Paukstis, G.L. (2000). Experimental analysis of an early life-history stage: selection on size of hatchling turtles. *Ecology* 81, 2290–2304.
- Keller, C. (1998). Assessment of reproductive state in the turtle *Mauremys leprosa*: a comparison between inguinal palpation and radiography. *Wildlife Research* 25, 527–531.
- King, R.B. (2000). Analyzing the relationship between clutch size and female body size in reptiles. *Journal of Herpetology* 34, 148–150.
- Lovich, J.E., Znari, M., Abdeljalil Ait Baamrane, M., Naimi, M., & Mostalich, A. (2010). Biphasic geographic variation in sexual size dimorphism of turtle (*Mauremys leprosa*) populations along an environmental gradient in Morocco. *Chelonian Conservation and Biology* 9, 45–53.

- Meek, R. (1987). Aspects of the population ecology of *Mauremys caspica* in north-west Africa. *Herpetological Journal* 1, 130–136.
- Pérez, M., Collado, E., & Ramo, C. (1979). Crecimiento de *Mauremys caspica leprosa* (Schweigger 1812) (Reptilia, Testudines), en la Reserva Biológica de Doñana. *Doñana Acta Vertebrata* 6, 161–178.
- Rollinson, N. & Brooks, R. J. (2008). Optimal offspring provisioning when egg size is “constrained”: A case study with the painted turtle *Chrysemys picta*. *Oikos* 117, 144–151.
- Ryan, K.M. & Lindeman, P.V. (2007). Reproductive allometry in the common map turtle, *Graptemys geographica*. *American Midland Naturalist* 158, 49–59.
- Schleich, H.H., Kastle, W. & Kabisch, K. (1996). *Amphibians and Reptiles of North Africa*. Koenigstein: Koeltz Scientific Publishers.
- Smith, C.C. & Fretwell, S.D. (1974). The optimal balance between size and number of offspring. *American Naturalist* 108, 499–506.
- van Loben Sels, R. C., Congdon, J.D., & Austin, J.T. (1997). Life history and ecology of the Sonoran mud turtle (*Kinosternon sonoriense*) in southeastern Arizona: A preliminary report. *Chelonian Conservation and Biology* 2, 338–344.

Accepted: 14 October 2011