Evolutionary Ecology Research, 2017, **18**: 539–554

Evolution of reproductive effort in mud turtles (Kinosternidae): the role of environmental predictability

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ABSTRACT

Question: Does environmental unpredictability drive the evolution of reproductive effort?

Data incorporated: We used life-history data from 31 kinosternid turtles. We tested relationships using the phylogenies of Iverson *et al.* (2013) and Spinks *et al.* (2014).

Methods: *Phylogenetically uncorrected*: We ran correlations between life-history traits and historic climatic variation. We used analysis of covariance (ANCOVA) to compare traits between temperate and tropical taxa. *Phylogenetically corrected*: We calculated independent contrasts and used the contrasts in correlations of life-history traits with historic climatic variation. To compare life-history traits between temperate and tropical taxa, we ran phylogenetic ANCOVAs and tested for phylogenetic signal.

Conclusions: Reproductive effort decreases with climatic variation. Temperate species evolved smaller clutches with large eggs and high reproductive effort. Tropical species from Mexico evolved larger clutches with medium-sized eggs and low reproductive effort.

Keywords: clutch size, egg size, phylogenetic comparative methods, relative clutch mass, temporal environmental variation.

INTRODUCTION

Energy budgets in iteroparous organisms are allocated along three main axes: growth, survivorship (including maintenance), and reproduction (Stearns, 1977, 1992; Congdon, 1989). When iteroparous organisms attain sexual maturity, a trade-off is made between energy invested in survivorship and that in reproduction based on environmental conditions and selection

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pressures. Some organisms invest more in reproduction, others in maintenance and survivorship (Lack, 1947; Cody, 1966; Stearns, 1992). When long-lived organisms invest comparatively more energy in survivorship than reproduction, they are considered to be bet-hedgers, a life-history strategy associated with many species of turtles, crocodilians, and large lizards (Enium and Fleming, 2004; Shine and Brown, 2008; Lovich *et al.*, 2015).

The reproductive outputs of oviparous reptiles are characterized by interactions of clutch size, clutch frequency, and egg size. Some species have large clutches composed of small eggs, while others have small clutches composed of large eggs (Tinkle, 1969; Tinkle *et al.*, 1970; Smith and Fretwell, 1974; Tinkle and Hadley, 1975; Moll, 1979; Elgar and Heaphy, 1989; Iverson *et al.*, 1993). Reproductive effort in a single bout is often measured as relative clutch mass [the ratio of clutch mass to maternal mass; for a discussion of the concept, see Cuellar (1984)]. How organisms allocate their reproductive effort throughout life will depend on environmental predictability (Roff, 1981, 2002), lineage effects (Brandt and Navas, 2011), and selection pressures experienced by the offspring (Reznick *et al.*, 1996, 2002).

Under temporal environmental variation, the trade-off between egg size and number of eggs in a clutch is determined (Stearns, 1976, 1989, 1992; Roff, 2002) by optimizing offspring (egg) size to increase offspring fitness, or by producing more offspring (eggs) to increase female fitness (Smith and Fretwell, 1974; Congdon and Gibbons, 1987; Macip-Ríos *et al.*, 2012). Murphy (1968) proposed a hypothesis to explain the evolution of reproductive effort. He predicted that under temporal environmental variation, organisms evolve to have low reproductive effort. The hypothesis assumes low survivorship in the developmental stages, high survivorship among adults, and an unpredictable environment. Despite the simplicity of Murphy's hypothesis, very few empirical studies have tested it in long-lived animals (Longhurst, 2002; Roff, 2002).

Good model organisms to test Murphy's hypothesis are freshwater turtles. Turtles are considered 'the paragon of long life' among animals (Gibbons, 1987; Wilbur and Morin, 1988), and have the lowest reproductive effort reported among vertebrates (Shine and Schwarzkopf, 1992; Macip-Ríos, 2010). Most populations show high mortality in the early stages of life (e.g. nest mortality), whereas after turtles attain a certain body size (shell size and thickness), survivorship is high (Iverson, 1991b).

Studies of turtle life-history evolution have focused on lifestyles – terrestrial, freshwater, and marine (Wilbur and Morin, 1988) – correlations between reproductive output traits (Iverson, 1992), and variation of clutch size and body size with latitude (Moyers-Arévalo, 2012). Indeed, reproductive output has been a common focus of turtle research over the last two decades (Iverson, 1992; Broderick *et al.*, 2003). This body of literature provides information that can be used for meta-analysis to test the reproductive effort hypothesis proposed by Murphy (1968).

We focused our research on an exclusively New World freshwater turtle family. The mud turtle family (Kinosternidae) has a distribution from southern Canada to northern Argentina and occurs in all kinds of aquatic environments throughout its range (Ernst and Barbour, 1988; Ernst and Lovich 2009; Legler and Vogt, 2013). The family has four recognized genera [but see Iverson *et al.* (2013) for the suggestion of a cryptic genus] and 28 species (41 taxa in total) (van Dijk *et al.*, 2014). Mexico is a hotspot of kinosternid diversity, with 19 species (21 taxa in total). Ninety per cent of kinosternid species occur both in Mexico and the USA, as do 100% of its genera.

Several studies have been published on mud turtle reproductive biology in North America in recent decades (Table 1). In this paper, our aim is to examine how temporal environmental variation affects the evolution of reproductive effort in mud turtles. We predict that reproductive output should match local environmental conditions. Specifically, small clutches of large eggs and high reproductive effort will be the norm in highly variable environments, whereas large clutches of small eggs and low reproductive effort are to be expected in stable (or more predictable) environments.

MATERIALS AND METHODS

Sampling and data analysis

We conducted an analysis to examine the evolution of reproductive effort with temporal environmental variation as the main factor. We gathered life-history data from published studies (Table 1) and from our own research (Macip-Ríos *et al.*, 2009, 2012, 2013; Vázquez-Gómez *et al.*, 2015). To infer temporal environmental variation, we used historical climate data for each of the localities where kinosternid studies have been conducted. We reviewed the literature with the aim of identifying studies that included the following information: relative clutch mass (RCM), body size (carapace length, CL), body mass, clutch size (CS), and egg width (EW). In some cases, we augmented the data with other related studies nearby, or used averaged values of body mass, egg mass, and clutch size (Table 1).

We gathered climate data from the precise locality (or localities) where each species/population (taxa from the published studies) was studied, or from the closest weather station. To estimate temporal environmental (climate) variation by study locality, we searched for two basic types of climatic variables: temperature (i.e. mean monthly temperature, minimum monthly temperature, maximum monthly temperature) and rainfall (i.e. total monthly rainfall, mean monthly evapotranspiration, maximum daily rainfall).

We calculated standard deviations for each climatic variable and then computed a mean of standard deviations for temperature and rainfall. Using this procedure, we created thermal variation (TV) and rainfall variation (RV) estimators. We also averaged the two, standard TV and standard RV, to create a single variable: total climatic variation (TCV).

The National Oceanic and Atmospheric Administration (NOAA online services) provided the climate data for the localities in the USA, while Servicio Meteorologico Nacional provided the climate data for Mexico. The range in climate data differed between weather stations, some weather stations having narrow datasets, others having broader datasets. All the stations provided data for a minimum of 20 years.

Analysis: statistical and comparative phylogenetic methods

To test Murphy's (1968) hypothesis, we used two different approaches: (1) a statistical approach that did not consider the phylogeny of mud turtles, and (2) a phylogenetic approach using two recent published phylogenies of the kinosternids (Iverson *et al.*, 2013; Spinks *et al.*, 2014). Both phylogenies offer robust data and have good support, but were generated with different phylogenetic inference methods, resulting in a debate that will continue until any discrepancies are resolved. We log-transformed the data to meet the assumptions of normality and linearize the correlations (Zar, 1999).

The branch lengths of Iverson *et al.* (2013) and Spinks *et al.* (2014) were not comparable since the two phylogenies were estimated using different methods (Garland *et al.*, 1999). Thus, to compare results from the comparative methods of the two topologies, we transformed branch lengths by: (1) equalizing branch lengths to unity and (2) using the Grafen (1989) method. We conducted our analysis with five datasets: two datasets using the topology of

Iverson *et al.* (2013), one with branch lengths equal to 1 and another with branch lengths estimated by the Grafen method; two datasets using the topology of Spinks *et al.* (2014), again one with branch lengths equal to 1 and another with branch lengths estimated by the Grafen method; and a fifth data set without the phylogenetic component.

As we did not have the same number of species in the two phylogenies, we pruned the phylogeny for *Kinosternon alamosae* reported by Spinks *et al.* (2014) and included soft polytomies when we had data for more than one population per species, such as *K. integrum*, *K. sonoriense*, *K. flavsescens*, and *Sternotherus odoratus*. Since we used data from different sources and two phylogenies, we proceeded to analyse all datasets for congruence, or at least similar tendencies, in the results (Logan, 2010).

We used Felsenstein's (1985) independent contrasts (FIC) with a regression to the origin (Felsenstein, 2008) to examine the correlation between reproductive effort and temporal environmental variation. FIC was designed as a trait vs. trait test, however we assumed phylogenetic niche conservatism (Cooper *et al.*, 2011; Crisp and Cook, 2012) and used temporal climatic variation as a set of variables tightly related to populations. We ran the FIC using TCV, TV, and RV as independent variables and each of the life-history traits previously described as dependent variables.

We ran an extra FIC that accounted for temperate and tropical species, in which we considered tropical species to be those below the Tropic of Cancer and temperate species to be those above the Tropic of Cancer. Based on the hypothesis of Morales-Verdeja and Vogt (1997), that temperate turtle species are mostly affected by temperature, while tropical (dry tropics in the case of Mexico) species are mostly affected by rainfall, we conducted the FIC using standard deviations of TV (SDTV) for temperate species and standard deviations of RV (SDRV) for tropical species. We performed FIC analyses with Mesquite v.3.04 (Maddison and Maddison, 2015) using the PDAP package (Garland *et al.*, 1999; Garland and Ives, 2000). We assessed the environmental temporal variation of tropical versus temperate species using two approaches: (1) correlating the environmental variables (TCV, TV, and RV) and (2) comparing the environmental variables (TCV, TV, and RV) between temperate and tropical localities.

To determine differences in life-history traits, we compared tropical and temperate species using a phylogenetic ANCOVA (Garland *et al.*, 1993), for which we used the phytools package (Revell, 2012) in R (R Development Core Team, 2008). We also ran a test of phylogenetic signal in phytools (Revell, 2012). We used the *K*-statistic (Blomberg *et al.*, 2003), which works as a gauge to estimate phylogenetic signal in a trait. Transformations, parametric assumptions tests, and standard statistical analyses were performed with JMP v.5.0.1 (SAS Institute, 2002). For all statistical analyses (phylogenetic and standard), we set $\alpha = 0.05$.

RESULTS

We used 31 taxa in our analysis [30 taxa for the topology of Spinks *et al.* (2014)]. The sample included mud turtles distributed from Nebraska, USA to Oaxaca, Mexico and it covered life-history data from 25° of latitude in North America. Data were not available for species in Central or South America. Table 1 summarizes our database and the data on life-history traits.

Among kinosternids, body size (CL) averaged 127.81 ± 56.49 mm (range 75–400 mm), clutch size averaged 4.0 ± 1.67 eggs (range 1–10 eggs), relative clutch mass averaged 0.077 ± 0.025 (range 0.03–0.11), and egg width averaged 17.01 ± 1.71 mm (range 14.1–24.0 mm).

Table 1. Life-history traits of the species and populations under study

Taxa	Exact locality	Relative clutch mass	Carapace length (mm)	Clutch size	Egg width (mm)	References
Claudius angustatus	El Jobo, Veracruz	0.0551	106.9	3	17.5	*Aguirre-Leon *et al*. (2002), *Espejel-González (2004)
Kinosternon abaxillare	Near Rio Cintalapa Bridge, Hwy 190, Chiapas	0.0965	118.6	3	17	Iverson (2010)
K. acutum	El Jobo, Alvarado, Veracruz	0.101	88.32	3	17	*Lopez-Luna (unpublished data); Legler and Vogt (2013)
K. alamosae	Alamos, Sonora	0.109	104.5	4	15.2	Iverson (1989a)
K. arizonense	Pima County, AZ	0.065	145.1	4.7	17.8	Iverson (1989b)
K. baurii	Alachua, Levy, and Marion Counties, FL	0.090	91.6	4	17.35	Iverson *et al.* (1991), Ewert and Wilson (1996), Nagle *et al*. (1998)
K. chimalhuaca	Chamela, Jalisco	0.071	139.87	4.3	17.89	Macip-Ríos *et al.* (2013)
K. creaseri	Coba, Quintana Roo	0.045	116	1	19.1	Iverson (1988)
K. flavescens	Gimlet Lake, Garden County, NE	0.109	102.5	6.5	16.13	Iverson (991a)
K. flavescens	Lubbock County, TX	0.119	106.3	4.86	16.6	Long (1986)
K. herrerai	Tres Ríos and Buena Vista, Veracruz	0.072	132.5	3.5	16.93	This paper
K. hirtipes	Galeana, Chihuahua	0.071	110.6	3	16.34	Iverson *et al.* (1991)
K. integrum	Tonatico, Edo. Mexico	0.043	142.7	4	17.15	Macip-Ríos *et al.* (2009)
K. integrum	Tejupilco, Edo. Mexico	0.079	142.7	4	17.62	Macip-Ríos *et al.* (2012)
K. integrum	Nuevo Urecho, Micchoacan	0.067	184.3	6.88	18.74	Macip-Ríos *et al.* (2013)
K. integrum	Playa Azul, Michoacan	0.072	161.5	5	16.57	Macip-Ríos *et al.* (2013)
K. integrum	Tres Palos, Guerrero	0.042	156.5	3.11	25.1	This paper

Table 1.—*continued*

Taxa	Exact locality	Relative clutch mass	Carapace length (mm)	Clutch size	Egg width (mm)	References
K. integrum	Sierra de Nanchititla, Edo. Mexico	0.061	132.5	4	17.23	This paper
K. leucostomum	Los Tuxtlas, Veracruz	0.030	145.39	2.24	19.3	Horne (unpublished data)
K. oaxacae	Pochutla, Oaxaca	0.049	121	4	17	Vazquez-Gómez *et al.* (2015)
K. subrubum subrubum	Ellenton Bay, SC	0.106	86.3	3.4	15.63	Gibbons (1983), Frazer (1991), Congdon and Gibbons (1985), Iverson *et al.* (1991)
K. scorpioides cruentatum	Coba, Quintana Roo	0.048	110	2.2	16.9	Iverson (2010)
K. sonoriense	Yavapai and Maricopa Counties, AZ	0.0735	119.5	4.05	14.38	Hulse (1982), Iverson *et al.* (1991)
K. sonoriense	Chiricahua Mountains, AZ	0.110	130	6.7	16.85	Van Loben Sels *et al.* (1997)
K. subrubum hippocrepis	Hot Springs, Garland County, AR	0.079	96.3	3.17	15.44	Iverson (1979)
Sternotherus carinatus	McCurtian County, OK	0.081	102	2.3	16.6	Iverson (2002)
S. carinatus	Garland, Montgomery, and Saline Counties, AR	0.092	117	3.8	17.2	Iverson (2002)
S. minor	Oviedo and Seminole Counties, FL	0.096	100.1	2.815	17.24	Iverson (1978)
S. odoratus	Ellenton Bay, SC	0.112	80	4.5	15.47	Congdon and Gibbons (1985), Iverson *et al.* (1991)
S. odoratus	7 km NW of Richmond, VA	0.104	74.9	4.1	14.1	Mitchell (1985a, 1985b, 1988)
Staurotypus triporcatus	Los Tuxtlas, Veracruz	0.043	400	9.8	24	*Vogt (1997), Legler and Vogt (2013)

*Estimated value from the literature.

Body size (coefficient of variation = 44) showed the largest amount of variation of the life-history traits analysed, closely followed by clutch size (CV = 41), reproductive effort (CV = 32), and finally egg width (CV = 10.4).

Similar results were observed in correlations between environmental variables and traits (see Table 2 for details) when using FICs with both the topologies of Iverson *et al.* (2013) and Spinks *et al.* (2014) and both branch lengths methods. We found consistent correlations across both topologies between clutch size and body size, and between egg width and body size (see Table 2 for details).

When we used Iverson and colleagues' (2013) topology with branch lengths equal to 1, relative clutch mass (reproductive effort) correlated negatively with rainfall variation ($r = -0.35$, $P = 0.06$) and with thermal/rainfall variation ($r = -0.35$, $P = 0.05$). When we used Spinks and colleagues' (2014) topology and branch lengths equal to 1, similar results were obtained ($r = -0.38$, $P = 0.03$ and $r = -0.4$, $P = 0.03$ respectively). When using Spinks and colleagues' topology with branch lengths equal to 1, we also observed a positive correlation between relative clutch mass and thermal variation ($r = 0.47$, $P < 0.01$) and a negative correlation between egg size and thermal variation ($r = -0.42$, $P = 0.01$).

When we used Grafen's (1989) branch length conversion, we observed a negative correlation between egg width and thermal variation both with Iverson and colleagues' topology ($r = -0.42$, $P = 0.01$) and that of Spinks *et al.* ($r = -0.47$, $P = 0.01$). Standard statistical analysis, uncorrected for phylogeny, revealed similar correlations between life-history traits and environmental variables. However, the standard statistical analysis detected multiple significant correlations for different combinations of variables with egg width, such as thermal variation, rainfall variation, and thermal/rainfall variation combined (Table 2).

The environmental variables showed significant correlations with latitude: total climatic variation (TCV) was negatively correlated ($r^2 = -0.23$, $P = 0.003$), thermal variation (TV) was positively correlated ($r^2 = 0.88$, $P < 0.0001$), and rainfall variation (RV) was negatively correlated ($r^2 = -0.44$, $P < 0.0001$) with latitude. When we compared tropical vs. temperate environments, tropical environments had higher TCV ($t_{18.51} = 3.24$, $P = 0.004$), TV ($t_{16.85} = 9.35$, $P < 0.0001$), and RV ($t_{17.62} = 5.06$, $P < 0.0001$) than temperate environments.

When comparing temperate and tropical species, we detected marked variation in reproductive effort (relative clutch mass) across all topologies and branch length conversion methods (Table 3). Temperate species (0.094 ± 0.01) showed significantly higher reproductive effort than tropical species (0.060 ± 0.02). Additionally, for Spinks and colleagues' (2014) topology and both branch length conversion methods, the egg widths of tropical species were greater than those of temperate species ($F = 9.9$, $P = 0.002$ and $F = 9.9$, $P = 0.001$ respectively). We also detected body size variation with Spinks and colleagues' topology with Grafen's branch length conversion when using the data set without the phylogenetic component (see Table 3 for details).

Egg width showed a high phylogenetic signal both with Iverson and colleagues' and Spinks and colleagues' topology with branch lengths equal to 1 ($K = 0.77$, $P = 0.005$ and $K = 0.72$, $P = 0.01$ respectively; see Table 4). Body size and relative clutch mass showed a more moderate phylogenetic signal when using Iverson and colleagues' topology with branch lengths equal to 1 ($K = 0.64$, $P = 0.018$ and $K = 0.61$, $P = 0.009$ respectively). For Spinks and colleagues' topology and branch lengths equal to 1, relative clutch mass showed a medium phylogenetic signal ($K = 0.41$, $P = 0.07$). In contrast, relative clutch mass showed a significant phylogenetic signal ($K = 0.17$, $P = 0.042$) when using Iverson and colleagues' topology and Grafen's branch length conversion. Body size showed a significant

Table 2. Felsenstein phylogenetic independent contrasts using the topologies of Iverson *et al.* (2013) ($n = 31$) and Spinks *et al.* (2014) ($n = 30$) in combination with two different branch length methods

		Iverson *et al.* BL = 1		Spinks *et al.* BL = 1		Iverson *et al.* BL = Grafen		Spinks *et al.* BL = Grafen		Standard statistical analysis	
Y	X	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
CL	Total climate variation	0.20	0.27	0.20	0.27	0.31	0.08	0.28	0.13	0.41	0.01
CL	Temperature variation	−0.24	0.18	−0.33	0.07	−0.29	0.10	−0.34	0.05	−0.42	0.01
CL	Rainfall variation	0.22	0.22	0.24	0.20	0.34	0.05	0.31	0.08	0.45	0.008
CL	Temperature/rainfall variation	0.25	0.16	0.27	0.15	0.39	0.03	0.36	0.04	0.47	0.006
CS	Total climate variation	0.16	0.38	−0.04	0.81	0.32	0.07	−0.02	0.90	0.00001	0.98
CS	Temperature variation	−0.15	0.39	−0.17	0.36	−0.26	0.14	−0.12	0.51	−0.025	0.38
CS	Rainfall variation	0.17	0.33	−0.004	0.98	0.36	0.04	−0.005	0.97	0.001	0.81
CS	Temperature/rainfall variation	0.05	0.78	0.004	0.98	0.20	0.91	−0.009	0.96	0.004	0.71
EW	Total climate variation	0.016	0.93	−0.04	0.80	0.27	0.13	0.21	0.25	0.11	0.06
EW	Temperature variation	−0.28	0.12	−0.42	0.01	−0.42	0.01	−0.47	<0.01	−0.16	<0.01
EW	Rainfall variation	0.037	0.84	0.08	0.64	0.28	0.12	0.21	0.24	0.16	0.02
EW	Temperature/rainfall variation	0.04	0.79	0.09	0.63	0.24	0.19	0.15	0.41	−0.018	0.01
RCM	Total climate variation	−0.26	0.14	−0.28	0.12	−0.17	0.33	−0.12	0.50	−0.24	0.005
RCM	Temperature variation	0.28	0.11	0.47	<0.01	0.25	0.16	0.21	0.25	0.46	<0.0001
RCM	Rainfall variation	−0.33	0.06	−0.38	0.03	−0.30	0.09	−0.24	0.19	−0.38	<0.0001
RCM	Temperature/rainfall variation	−0.35	0.05	−0.40	0.03	−0.142	0.45	−0.18	0.50	0.46	<0.0001
CS	CL	0.75	<0.0001	0.74	<0.0001	0.79	<0.0001	0.79	<0.0001	0.67	<0.0001
EW	CL	0.78	<0.0001	0.79	<0.0001	0.84	<0.0001	0.85	<0.0001	0.79	<0.0001
RCM	CL	−0.22	0.22	−0.24	0.18	−0.18	0.33	−0.19	0.29	−0.46	0.007
EW	CS	0.052	0.78	0.069	0.71	0.04	0.79	0.092	0.62	0.0008	0.87
RCM	EW	−0.22	0.22	−0.27	0.22	−0.17	0.36	−0.16	0.37	−0.23	<0.0001
RCM	CS	−0.25	0.16	−0.14	0.44	−0.35	0.05	−0.04	0.08	−0.038	0.28

Note: Branch lengths (BL) are presented as BL = 1 (branch lengths all equal to 1) or BL = Grafen [branch lengths estimated by the Grafen (1989) method]. CL = carapace length, CS = clutch size, EW = egg width, RCM = relative clutch mass.

Table 3. Phylogenetic ANOVA results of the comparisons between temperate and tropical populations of kinosternids

Trait	Temperate species (mean ± SD)	Tropical species (mean ± SD)	Iverson *et al.* BL = 1		Spinks *et al.* BL = 1		Standard statistical analysis	
			F	*P*	*F*	*P*	*F*	*P*
CL	104.44 ± 18.49	149.92 ± 70.68	10.51	0.10	13.50	0.001	5.82	0.02
CS	4.12 ± 1.22	3.93 ± 2.03	0.66	0.68	1.95	0.24	0.09	0.76
RCM	0.094 ± 0.01	0.060 ± 0.02	23.17	0.019	20.80	0.001	24.69	<0.0001
EW	16.15 ± 1.09	17.81 ± 1.93	9.35	0.12	9.90	0.002	8.43	0.007

Trait	Temperate species (mean ± SD)	Tropical species (mean ± SD)	Iverson *et al.* BL = Grafen		Spinks *et al.* BL = Grafen	
			F	*P*	*F*	*P*
CL	104.44 ± 18.49	149.92 ± 70.68	10.51	0.14	13.50	0.001
CS	4.12 ± 1.22	3.93 ± 2.03	0.66	0.72	1.9	0.19
RCM	0.094 ± 0.01	0.060 ± 0.02	23.17	0.019	20.80	0.001
EW	16.15 ± 1.09	17.81 ± 1.93	9.35	0.18	9.9	0.001

Note: Branch lengths (BL) are presented as BL = 1 (branch lengths all equal to 1) or BL = Grafen [branch lengths estimated by the Grafen (1989) method]. CL = carapace length, CS = clutch size, EW = egg width, RCM = relative clutch mass.

Table 4. Phylogenetic signal analysis of life-history traits among the kinosternids of North America

Trait	Iverson *et al.* BL = 1		Spinks *et al.* BL = 1		Iverson *et al.* BL = Grafen		Spinks *et al.* BL = Grafen	
	K	*P*	*K*	*P*	*K*	*P*	*K*	*P*
CL	0.64	0.018	0.32	0.17	0.12	0.37	0.28	0.02
CS	0.30	0.28	0.29	0.28	0.10	0.55	0.21	0.17
RCM	0.61	0.009	0.41	0.07	0.17	0.042	0.17	0.094
EW	0.77	0.005	0.72	0.01	0.14	0.13	0.15	0.25

Note: Branch lengths (BL) are presented as BL = 1 (branch lengths all equal to 1) or BL = Grafen [branch lengths estimated by the Grafen (1989) method]. CL = carapace length, CS = clutch size, EW = egg width, RCM = relative clutch mass.

phylogenetic signal ($K = 0.28$, $P = 0.02$) for Spinks and colleagues' topology and Grafen's branch length conversion.

DISCUSSION

Among the kinosternids, the most labile traits appear to be reproductive effort and egg size. Both traits were correlated with environmental factors, i.e. temperature and rainfall. These results support Murphy's (1968) hypothesis, which predicts a detectable reduction in reproductive effort when long-lived organisms inhabit temporally variable habitats. According to

Roff (2002), no study has shown statistical support for Murphy's hypothesis. However, we conducted meta-analysis without phylogenetic contrasts and two types of phylogenetic comparative methods, all of which confirm Murphy's (1968) predictions. Recently, Lovich *et al.* (2015) provided data that corroborate Murphy's (1968) predictions in a desert tortoise (*Gopherus agassizii*), a bet-hedging species that produces relatively small clutches of large eggs in a variable environment. Our approach was to explore the evolution of reproductive output across the kinosternid phylogeny, thus when interpreting our results consideration should be given to the correlations of traits evolving together as a life-history strategy (Roff, 2002), which is also driven by morphological and phylogenetic constraints (Congdon and Gibbons, 1987; Lovich *et al.*, 2012; Macip-Ríos *et al.*, 2012, 2013; Naimi *et al.*, 2012).

The correlation of clutch size/egg width with body size confirms a common trend in the reproductive ecology of turtles (Wilbur and Morin, 1988; Iverson, 1992; Ryan and Lindeman, 2007; Macip-Ríos, 2010). It seems that producing more eggs per clutch is a direct response of larger body size (Congdon and Gibbons, 1985; but see Ryan and Lindeman, 2007). However, according to our results, egg size (width) did not correlate in any way with clutch size as would be expected by the typical trade-off between size and number of offspring (Smith and Fretwell, 1974; Stearns, 1989). This result is at odds with previous life-history studies in turtles (Wilbur and Morin, 1988) in which lifestyle (terrestrial, marine, and freshwater) was considered the main factor in life-history variation. According to our data, changes in body size could be the primary response to environmental variation across this lineage of turtles.

The general trend we find in our dataset is that temperate kinosternids tend to be smaller in size and lay small eggs with clutch sizes proportional to their body size, whereas tropical species lay larger eggs in clutches that are slightly larger proportional to their body size (see Table 3). These patterns suggest that thermal ecology should be explored to determine if it is related to reproductive output (Shine and Schwarzkopf, 1992) in kinosternids. Reproductive effort (relative clutch mass) showed a notable difference between tropical and temperate species as well. Tropical species invest less body mass (average 6%) than temperate species (average 9.5%), which indicates that tropical lineages (which inhabit more temporally variable environments) evolved lower reproductive effort than temperate lineages (which inhabit less temporally variable environments), thus providing support for Murphy's hypothesis of reproductive effort.

Northern species tend to lay more eggs that are small enough to pass through their pelvic opening, and invest nearly 10% of their body mass by clutch (see Table 1 for references and Table 3 for data analysis). Northern species become reproductive at smaller sizes compared with tropical species (Wilbur and Morin, 1988; Iverson, 1992). Therefore, once they reach reproductive size, they invest energy in reproduction over the short reproductive season (May to September) and in survivorship during long overwintering or aestivating periods (September to May).

The offspring of temperate species are faced with adverse thermal conditions when they hatch in early fall [i.e. September (Lovich *et al.*, 2014)] or overwinter in the nest until they emerge in mid-spring [i.e. late May (Gibbons and Nelson, 1978)]. Female kinosternids from northern latitudes invest more energy in reproductive effort (relative clutch mass) than those in the dry tropics further south (see Tables 2 and 3). Northern species/populations face harsh thermal (extreme) conditions, but because of little variation in rainfall throughout the year these habitats are predictable, with turtles experiencing manageable environmental conditions from April to October, although hatchlings do need more energy for overwintering. In contrast, because southern species/populations of kinosternid turtles in the Mexican dry tropics experience less variable temperatures, and rainfall is restricted to the rainy season (average from June to October), with significant variation in the length of the wet season among years, lower reproductive effort invested in large clutches with medium-sized eggs seems a reasonable strategy to adopt.

Tropical species evolved larger body sizes due to longer growing seasons and less variable thermal conditions. This allows them to produce slightly larger eggs than temperate species, with almost the same clutch sizes proportional to their body size. We detected remarkably low investment in the clutches of tropical species compared with temperate species. In other words, dry tropics species produce clutch sizes and eggs in line with their body size, but spend significantly less energy on reproductive effort (relative clutch mass) than the northern species.

The combination of life-history traits of tropical species seems to be optimal for long growing seasons (March to late November) but only under very high environmental variability. In the dry and wet tropics, water availability can fluctuate significantly within and between years (the rainy season fluctuates from early June to early October), a factor that will affect hatchling survivorship in two ways: prolonged droughts that destroy nests and hatchlings, or heavy or unusual rains that flood nests and kill developing, aestivating or overwintering offspring.

Our analysis of climate data confirms stronger correlations for tropical species with environmental variation. For the tropical kinosternids in Mexico, rainfall – which shows much greater variation than temperature – seems to be the main factor. In contrast, the northern species face shorter breeding seasons and more stressful thermal environments (but less variation in rainfall). This is what Morales-Verdeja and Vogt (1997) hypothesized about life-history traits in freshwater turtles.

Turtles evolved variation of the same general life-history strategy to fit cold, predictable, short breeding seasons in temperate regions versus warm, less predictable, but longer breeding seasons in the dry tropics. We lacked data from Central America and South America, where temporal environmental variation in temperature and rainfall tends to be more stable and predictable as one approaches the equator.

For species/populations under these environmental conditions, Murphy's (1968) hypothesis predicts higher reproductive effort if environmental variation affects hatchling mortality; however, some species from South America, such as *Kinosternon scorpioides scorpioides* and *K. leucostomum* spp., achieve relatively large sizes among their lineage, but no data on their reproductive effort are available. According to Murphy (1968) and others (Williams, 1966; Goodman, 1974, 1979; Longhurst, 2002), reproductive effort should be independent of body size and must be reduced gradually as temporal environmental variation affects survivorship of hatchlings/young, however our data indicate that reproductive effort was affected by body size.

Body size variation across the kinosternid lineage may be due to an effect of phylogenetic inertia, which is expected for this trait (Blomberg *et al.*, 2003) and other traits greatly affected by body size, such as clutch size and egg width. For the estimation of phylogenetic inertia by phylogenetic signal (Table 4) there was no consistency in the results, but there were high levels of phylogenetic signal for body size and for egg size (egg width). Reproductive effort (relative clutch mass) also showed intermediate to low phylogenetic signal depending on the topology used. It would appear that clutch size is a trait strongly related to environmental and morphological traits.

Our data followed the expected pattern of Murphy's hypothesis, even in weak correlations (due to the nature of the sample and sample size) that were statistically significant.

Using two recent published phylogenies of the kinosternids (Iverson *et al.*, 2013; Spinks *et al.*, 2014), we provided support by finding similar trends for each, but complicated other interpretations such as phylogenetic signal. When we transformed branch lengths to unity or using the Grafen method, the latter only allowed for the detection of strong correlations. On the other hand, when we converted branch lengths to 1, this method detected a broad range of correlations, but with more statistical rigour than the non-phylogenetic statistical analyses. The topologies of Spinks *et al.* (2014) and Iverson *et al.* (2013) led us to similar conclusions and the ambiguous interpretation of results due to topology was minimal (but see Table 2).

We conclude that reproductive output in kinosternids has evolved as a bet-hedging life-history strategy that is exacerbated in the dry tropics compared with temperate regions. What should be the pattern for the wet tropics species/populations near the equator? More data are needed for species and populations near the equator to understand the response in the wet tropics. We hypothesize that equatorial species should be intermediate between temperate and dry tropics species, since temperature tends to be more stable throughout the year and rainfall is perennial rather than seasonal.

ACKNOWLEDGEMENTS

We thank Brian Horne and Marco Antonio López-Luna for sharing their unpublished data on *Kinosternon leucostomum* and *K. acutum* respectively. Victor H. Sustaita, Gabriel Barrios, and Pablo Brauer helped with fieldwork from 2006 to 2009. CONACyT provided R.M.-R. with a graduate studies scholarship from 2006 to 2010. We also thank Posgrado en Ciencias Biológicas (School of Biological Graduate Studies) of Universidad Nacional Autónoma de México for their support. Darrel Frost and Mike Jones made important comments during this project. This paper was written during R.M.-R.'s first year as Associate Professor with ENES-Morelia, UNAM. R.M.-R. thanks Professor Ken Oyama for his support. An earlier version of the manuscript benefited from comments of Jeffrey Lovich.

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