GLOBAL CORRELATES OF SPECIES RICHNESS IN TURTLES

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ABSTRACT

The relationships between maximum total and maximum freshwater turtle species richness versus twelve environmental factors hypothesized to be correlated with richness were examined for 42 river drainage basins on five continents. The only highly significant correlate was annual rainfall. Latitude, temperatures, and basin area and discharge were not significantly correlated with species richness. These results are interpreted in light of current theoretical determinants of species diversity.

INTRODUCTION

Although some authors have provided gross descriptions of global species richness patterns in turtles (e.g. Darlington, 1948, 1957; Mittermeier, 1972; Pritchard, 1979), quantitative analysis of richness patterns is available only on local geographic scales (e.g. Huheey, 1965, for Illinois; Rogers, 1976; Owen & Dixon, 1989, for Texas; Schall & Pianka, 1978, for Iberia). Quantitative work on a broader scale has been impeded by the lack of published information on the precise distributions of many of the world's turtles. The publication of preliminary distribution maps for all turtle species (Iverson, 1986) now makes a quantitative study of the correlates of global turtle species richness possible.

This study was undertaken to test several specific predictions about expected correlates with species richness that were based on biogeographic theory and/or patterns observed in other vertebrate taxa. I hypothesized that species richness should be greatest in the tropics (e.g. see Pianka, 1966; Kiester, 1971; MacArthur, 1972; Schall & Pianka, 1977; Stevens, 1989); in drainage basins with large areas (e.g. see Swift *et al.*, 1986; McAllister *et al.*, 1986; Angermeier & Schlosser, 1989) or with large discharge rates (e.g. Livingstone *et al.*, 1982); in areas with warmer winter and/or summer temperatures (Schall & Pianka, 1977, 1978); or with a low annual range of temperature variation (Schall & Pianka, 1977, 1978); and in areas with high rainfall (Rogers, 1976; Schall & Pianka, 1978; Owen & Dixon, 1989) or low seasonal variation in amount of rain. These predictions are here tested with maximum species richness data for 42 drainage basins representing all continents inhabited by turtles.

METHODS

Turtle species density maps were prepared by outlining the range of each turtle species as plotted in Iverson (1986), and manually overlaying those range maps to produce species richness isopleth (= species density) maps by turtle family and continent (Iverson, 1992). Approximately 60 river basins representing the major drainages on every continent were selected for analysis, and the site of maximum total (i.e. freshwater and terrestrial) turtle species richness in each basin pinpointed. The following environmental variables were compiled from records from the city nearest to that site as reviewed in Ruffner (1978) or Ruffner & Bair (1987): mean daily maximum and minimum temperatures in winter and summer (January or July, depending on hemisphere), difference in mean daily temperature in summer (January or July) compared to that in winter (a measure of seasonal variation in temperature), mean annual rainfall, mean monthly rainfall in the wettest month, mean monthly rainfall in the driest month, and the difference in mean rainfall in the wettest month compared to that in the driest month.

Drainage area and discharge data for each basin were then compiled, primarily from Showers (1973), but checked and supplemented when necessary with data from Tamayo and West (1964), Snead (1980), Berra (1981), Livingstone *et al.* (1982), and Swift *et al.* (1986). In addition to maximum total species richness for each basin, aquatic species richness was also determined for the same location based on habitat preferences in Ernst & Barbour (1989). Species richness in each of the (primarily aquatic) families Chelidae (Austro-American sidenecked turtles), Pelomedusidae (Afro-American sidenecked turtles), Kinosternidae (American mud and musk turtles), Trionychidae (Softshell turtles), Bataguridae (Batagurine turtles) and Emydidae (Pond turtles) were also determined for the same location. A nearly complete data set was thus compiled for a total of 42 basins (Appendix 1).

Although the data set is possibly flawed by (1) assuming the accuracy of distributions plotted by Iverson (1986); (2) using only the location of maximum richness in each basin; and (3) being forced to use climatic data from the nearest large city for which records are available (and thus not precisely at the location of maximum diversity), it is believed to be representative enough to be of value in this preliminary investigation of global correlates of species density in turtles. Correlation analysis between environmental variables and species richness values was performed with Statview™ Software on a Macintosh™ computer. Because 12 correlations were generated for each taxonomic group, the significance level was adjusted to $P < 0.004$ (0.05/12) to account very conservatively for the experiment-wise error rate (Sokal & Rohlf, 1981).

RESULTS

Turtle species richness is greatest in the lower Ganges-Brahmaputra river basin in India and Bangladesh (ca. 23° N latitude; seventeen aquatic and two terrestrial species) and in the lower Mobile River basin in Alabama in the United States (ca. 31°N latitude; sixteen aquatic and two terrestrial; see also Iverson, 1992). The results of the correlation analysis of total species richness, total aquatic species richness, and within family species richness versus the twelve environmental characters (Table 1) reveal that the only consistent predictor of species richness was annual rainfall (Fig. 1).

Annual rainfall was significantly correlated with species richness for all taxa combined, for all aquatic taxa combined, for trionychids, and for all non-trionychid taxa combined (Table 1). Only trionychid richness was positively correlated with seasonal variance in rainfall.

Surprisingly, neither latitude nor basin area nor discharge rate were significantly correlated with species richness in any group. Of the several measures of temperature, none showed a significant correlation with species richness for any taxonomic group, although the relationships between winter temperature and total and trionychid species richness approaches significance. Precipitation amount during the wettest month is positively correlated with overall species richness, but among families, only with trionychid richness. Precipitation during the driest month is positively correlated with richness for emydid turtles and all aquatic non-trionychid turtles combined. When the effects of latitude were removed by partial correlation analysis, only total annual rainfall ($r = 0.55$; $P< 0.0001$) and driest month rainfall ($r = 0.51$; $P= 0.0005$) were significantly correlated with total species richness.

DISCUSSION

Few of my original predictions were supported by the data compiled here. Perhaps the most surprising is the weak correlation between richness and latitude; however, this may be related to the lack of a continental land mass between about 10° N and 10°S latitude in the Oriental zoogeographic region. In addition, within-family patterns are complicated because some families are high-latitude families that have only recently dispersed into the tropics (e.g. the Kinosternidae and Emydidae, which both evolved primarily in isolation in North America; Darlington, 1948, 1957). Thus richness in these families is not inversely correlated with latitude (or positively correlated with winter temperatures); indeed, the signs of the correlation coefficients (though not statistically significant) are the opposite of those predicted.

Given that freshwater fish species richness has been found to be correlated with both lake (Barbour & Brown, 1974) and basin area (McAllister et al., 1986; Swift et al., 1986), as well as basin discharge (Livingstone et al., 1982), it was surprising that neither basin area nor basin discharge were positively correlated with turtle species richness at any taxonomic level. This may be because the richness value used in this analysis represents only the maximum local value for a particular basin and not the total for the entire basin; however, given the distributions figured by Iverson (1986), it is doubtful that even total turtle species diversity for each basin would be correlated with basin area.

Schall & Pianka (1977, 1978) have shown that turtle species density is positively correlated with mean July temperature in Iberia and mean annual temperature in the United States and Australia. However, my global analysis does not reinforce the effect of temperatures (summer, winter or annual) on density, except that winter temperatures and annual seasonality in temperature approach being significantly correlated with trionychid species richness. This is particularly interesting since the family Trionychidae is atypical among turtles in lacking temperature-dependent sex determination (Ewert & Nelson, 1991) and apparently lacking the ability of hatchlings to overwinter in the nest in temperate regions (Gibbons & Nelson, 1978). Whether these characteristics are related must await further study. Comparisons of correlation coefficients of the various measures of temperature with species richness for the various samples (even though not statistically significant at $P< 0.004$) do suggest that summer temperatures have less affect on turtle species richness than winter temperatures.

Rogers (1976, in Texas), Schall & Pianka (1978, in the United States and Australia) and Owen & Dixon (1989, in Texas) all demonstrated a positive correlation between turtle species richness and annual precipitation, although Schall & Pianka (1977) found the opposite trend in Iberia. However, the latter is obviously an artifact of the peninsular nature of Iberia as well as the multitude of mountain barriers that prevent dispersal away from the Mediterranean coastal plain. Schall & Pianka (1978) also noted a negative correlation between richness and variability in precipitation across years. The strongest correlations revealed in this study related turtle species richness to annual rainfall. However, although I had predicted that seasonal (i.e. within year) variation would be inversely correlated with richness (the climatic stability hypothesis; see Pianka, 1988), the actual pattern may be exactly the opposite (at least for some taxa).

The positive effects on richness of both amount of and seasonal variation in rainfall (though the latter may only affect the trionychids) provide some support for the spatial heterogeneity hypothesis (Pianka, 1988). More rain and more seasonality in rain presumably would result in more variety in habitats through the course of a year - from rivers, streams, lakes, and ponds to marshes and bogs, to meadows and ephemeral pools. In addition, more rain and more seasonality in rain within a basin (e.g., the Irawaddy, Mekong, and Ganges basins) also imply a greater likelihood of habitat disturbance through flooding, and thus the disturbance hypothesis (e.g. see Petraitis et al., 1989) may also be supported by these data. These basins indeed do have very high turtle species densities, with the world's highest being in the lower Ganges-Brahmaputra basin. However, further study will be necessary to test adequately the applicability of either the spatial heterogeneity or disturbance hypotheses.

Unfortunately, the data so far available on other factors do not permit a testing of several of the mechanisms hypothesized to explain diversity (reviewed by Pianka, 1988), e.g., the evolutionary time hypothesis, the ecological time hypothesis, the productivity hypothesis (see Currie, 1990), the competition hypothesis, the predation hypothesis (see Arnold, 1972), the climatic stability and stability in primary production hypotheses (see Pianka, 1966, 1988), and the climatic predictability hypothesis (though the latter might be tested with annual flood stage data). They also give no hint as to why the maximum diversity of turtles today (13 genera in the lower Ganges) was so far exceeded by diversity in Montana (ca. almost 48°N latitude) during the Upper Cretaceous (at least 18 genera and subgenera in the Hell Creek formation; Hutchison & Archibald, 1984), especially when at least 72-83% of Cretaceous taxa survived the Cretaceous-Tertiary boundary event (Hutchison & Archibald, 1984).

In summary, although a latitudinal gradient in species richness has been demonstrated for numerous plant and animal taxa (review in Stevens, 1989), no such pattern is evident in turtles. Likewise, although basin area and discharge are often highly correlated with species density in other aquatic taxa (e.g. Livingstone et al., 1982; Swift et al., 1986; McAllister et al., 1986; and Angermeier &
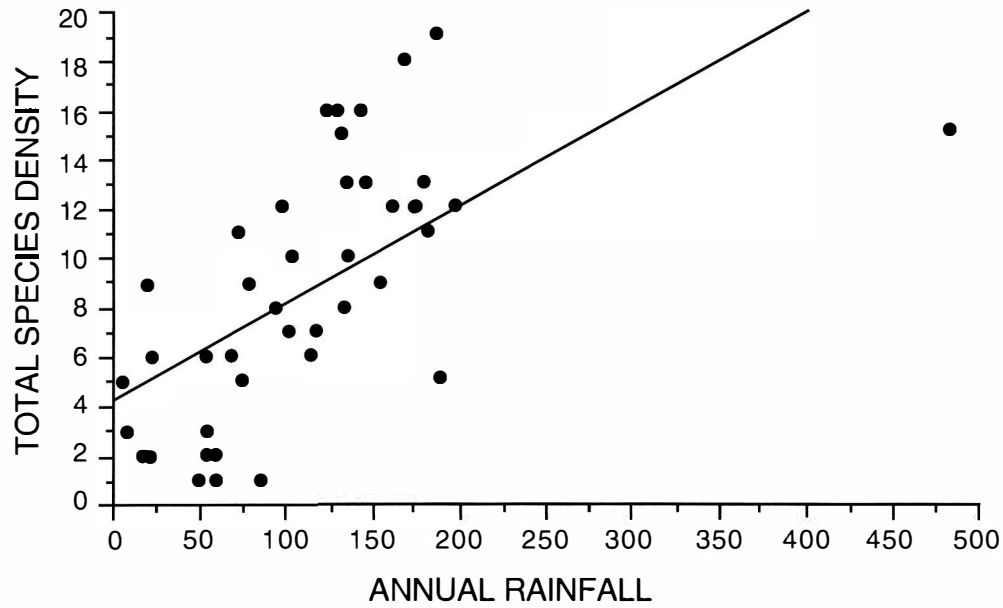
Fig. 1. Relationship between annual rainfall (mm) and maximum species richness for 42 river basins. Least squares regression equation is $y = 0.039x + 4.303$ ($N = 42$; $r = 0.62$; $P < 0.0001$).

Level of species Richness

Factor	Overall (N=42)		Aquatic (N = 42)		Chelid (N = 7)		Pelomedusid (N = 10)		Kinosternid (N = 14)		Trionychid (N = 28)		Batagund (N = 15)		Emydid (N = 16)		All aquatic but Trionychid (N = 42)	
	r	P	r	P	r	P	r	P	r	P	r	P	r	P	r	P	r	P
Latitude	-0.37	0.016	-0.29	0.06	-0.18	0.70	-0.71	0.023	+0.34	0.23	-0.44	0.020	-0.14	0.62	+0.03	0.92	-0.23	0.15
Basin area	+0.08	0.62	+0.09	0.58	+0.51	0.25	+0.59	0.08	-0.42	0.14	+0.05	0.82	-0.17	0.55	-0.01	0.96	+0.11	0.50
Discharge	+0.22	0.18	+0.26	0.12	+0.51	0.25	+0.27	0.48	-0.41	0.14	+0.26	0.21	-0.08	0.80	-0.15	0.57	+0.30	0.06
Winter max	+0.42	0.006	+0.34	0.029	+0.20	0.66	+0.50	0.15	-0.09	0.75	+0.52	0.005	+0.24	0.39	-0.08	0.77	+0.27	0.08
Winter min	+0.38	0.013	+0.31	0.049	+0.08	0.86	+0.27	0.45	-0.19	0.52	+0.50	0.007	+0.20	0.48	-0.26	0.33	+0.26	0.10
Sum max	+0.09	0.57	+0.16	0.31	+0.65	0.12	+0.29	0.42	+0.15	0.61	-0.22	0.27	-0.23	0.41	+0.25	0.35	+0.17	0.29
Sum min	+0.30	0.054	+0.33	0.031	-0.01	0.98	+0.07	0.84	+0.16	0.59	+0.26	0.19	+0.23	0.40	+0.14	0.61	+0.27	0.09
Seasonal difference	-0.35	0.023	-0.26	0.10	-0.14	0.77	-0.25	0.49	+0.23	0.42	-0.50	0.007	-0.23	0.41	+0.37	0.16	+0.22	0.17
Total rain	+0.62	0.001	+0.60	0.001	+0.10	0.83	+0.74	0.015	+0.12	0.68	+0.53	0.004	+0.59	0.022	+0.61	0.012	+0.52	0.0004
Wettest month	+0.45	0.003	+0.42	0.006	-0.30	0.52	+0.39	0.27	+0.05	0.87	+0.56	0.002	+0.47	0.08	+0.33	0.22	+0.30	0.06
Driest Month	+0.36	0.02	+0.41	0.007	+0.09	0.85	+0.49	0.15	+0.19	0.51	-0.23	0.24	-0.10	0.72	+0.68	0.004	+0.53	0.0003
Seasonal range	+0.41	0.007	+0.37	0.016	-0.33	0.46	+0.33	0.36	+0.01	0.97	+0.57	0.002	+0.48	0.07	+0.14	0.61	+0.24	0.13

TABLE 1. Correlations among measures of turtle species richness and environmental factors (see text for explanations). N = number of basins in sample. Statistical significance including experiment-wise error rate is $P < 0.05/12$ or $P < 0.0042$ (see text).

Schlosser, 1989), these relationships are also lacking among turtles. The only consistent correlate of turtle species richness identified in this study was total annual rainfall. Unfortunately, the precise mechanism through which rainfall might affect turtle diversity is not yet clear. However, even that variable explains only about 38% of the variation in turtle species richness in the 42 basins sampled, suggesting that other factors (e.g., dispersal history or past environmental conditions) may be more important in determining turtle species richness than those discussed here.

ACKNOWLEDGEMENTS

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APPENDIX 1.

Species density and environmental data for 42 river basins. Temperatures are in Celcius; rainfall in cm.

Basin	Contin-nent[a]	Climate data source	Lati-tude	Basin area (x 1000 km²)	Basin discharge (x 100 m³/sec)	Mean daily temperature[b]				Range annual monthly mean	Mean ann-ual rain	Mean monthly rainfall			Total turtle species	Aquatic turtle species
						Winter max[b]	Winter min[b]	Summer max[b]	Summer min[b]			Wettest month	Driest month	Range		
Amazon	NA	Manaus	3	6150	1750	31.7	23.9	33.9	23.9	1.1	181.1	26.2	3.8	22.4	13	12
Amur	AS	Khabarovsk	48	2050	98	-18.9	-25.0	23.9	17.2	42.5	48.8	10.4	0.5	9.9	1	1
Apalachicola	NA	Apalachicola	30	49	6	16.7	8.9	31.1	23.9	14.7	142.7	21.6	6.1	15.5	16	15
Chao Phyra	AS	Bangkok	14	150	—	31.7	19.4	32.2	24.4	2.8	146.8	35.6	0.3	35.3	13	11
Colorado	NA	Yuma	33	637	1	19.4	4.4	41.7	26.1	21.9	7.6	1.3	0	1.3	3	2
Congo	AF	Leopoldville	4	3822	390	27.2	17.8	30.6	21.1	3.3	135.4	19.6	0.3	19.3	10	8
Danube	EU	Bucharest	44	773	64	0.6	-6.7	30.0	16.1	23.3	57.9	9.7	2.8	6.9	2	1
Fly	AU	Port Moresby	9	55	90	28.3	22.8	31.7	24.4	0.8	101.1	19.3	1.8	17.5	7	7
Ganges	AS	Dacca	24	1621	385	25.0	13.3	31.7	26.1	9.7	187.7	33.8	0.5	33.3	19	17
Indus	AS	Karachi	25	1178	36	25.0	12.8	32.8	27.2	11.1	19.8	8.1	0.3	7.9	9	7
Irawaddy	AS	Moulmein	17	409	127	31.7	18.3	28.3	23.3	0.8	483.1	120.7	0.5	120.1	15	12
Kristna	AS	Hyderabad	17	259	—	29.4	15.0	30.6	22.8	4.4	75.2	16.5	0.8	15.7	5	4
Magdalena	SA	Cartagena	10	260	80	28.9	22.8	31.1	25.6	2.5	93.5	27.4	0	27.4	8	7
Mekong	AS	Saigon	11	811	120	31.7	21.1	31.1	23.9	1.1	198.4	33.5	0.3	33.3	12	10
Mississippi	NA	Little Rock	35	3222	173	10.0	-1.1	33.9	21.7	23.4	125.0	13.7	7.2	6.5	16	15
Mobile	NA	Mobile	31	111	11	16.1	5.0	32.8	22.8	17.2	170.2	22.6	6.6	16.0	18	16
Murray-Darling	AU	Adelaide	35	1072	4.7	15.0	7.2	30.0	16.1	11.7	53.6	7.6	1.8	5.8	3	3
Narmada	AS	Ahmadabad	23	98	12.3	29.4	14.4	33.9	26.1	8.1	74.4	31.0	0	31.0	5	4
Niger	AF	Enugu	6	2092	57	32.2	22.2	28.3	21.7	2.2	181.6	32.5	1.3	31.2	11	8
Nile	AF	Lira	2	2802	26	32.8	16.1	27.2	16.1	2.8	154.2	25.4	1.8	23.6	9	6
Orange	AF	Port Nolloth	29	677	3	16.7	7.2	19.4	11.7	3.6	5.8	0.8	0.3	0.5	5	1
Orinoco	SA	Bolivar	8	880	180	32.2	22.2	32.2	23.9	0.8	97.3	18.0	1.8	16.3	12	10
Parana	SA	Buenos Aires	27	3100	229	21.7	11.7	33.9	21.7	11.1	117.9	14.2	3.8	10.4	7	6
Po	EU	Venice	45	75	15	6.1	0.6	27.8	19.4	20.3	84.8	9.4	5.1	4.3	1	1
Potomac	NA	Washington	39	36	3.1	6.7	-1.1	30.6	20.6	22.8	103.6	12.4	6.4	6.1	10	9
Red	AS	Hanoi	21	120	—	20.0	14.4	33.3	26.1	12.5	176.3	38.6	2.0	36.6	12	10
Rhone	EU	Marseille	43	99	15	11.7	3.3	25.6	14.4	12.5	58.9	9.4	1.5	7.9	1	1
Rio Grande	NA	Brownsville	26	471	1	21.7	11.1	33.9	24.4	12.8	68.3	12.7	2.5	10.2	6	4
Sao Francisco	SA	Benin	13	611	27	26.1	20.6	30.0	23.3	3.3	190.0	28.4	6.6	21.8	5	3
Savannah	NA	Savannah	32	26	3.2	16.1	3.9	32.8	21.7	17.2	130.0	20.1	4.8	20.3	16	14
Senegal	AF	Dakar	15	440	—	26.1	17.8	31.1	24.4	5.8	54.1	25.4	0	25.4	6	4
Si	AS	Canton	23	448	116	18.3	9.4	32.8	25.0	15.0	161.5	26.9	2.3	24.6	12	12
St. Johns	NA	Jacksonville	30	21	0.9	19.4	7.2	33.3	22.8	14.7	136.1	19.6	4.3	15.2	13	11
St. Lawrence	NA	Detroit	42	1316	130	0	-7.2	28.3	17.2	24.7	78.7	8.6	4.6	4.1	9	8
Suwannee	NA	Gainesville	29	23ᶜ	4	20.6	8.3	32.8	21.7	12.6	133.4	19.6	4.6	15.0	15	13
Tigris	AS	Abadan	30	1105	28.6	17.8	6.7	44.4	27.2	23.6	19.3	4.6	0	4.6	2	2
Volga	AS	Astrakhan	46	1380	77	-5.0	-10.0	29.4	20.6	32.5	16.3	1.8	1.0	0.8	2	1
Volta	AF	Accra	5	388	11.7	30.6	22.8	27.2	22.8	1.7	72.4	17.8	1.5	16.3	11	8
Yangtze	AS	Shanghai	31	1827	322	8.3	0	32.8	23.9	24.2	114.3	17.8	3.8	14.0	6	6
Yaqui	NA	Guaymas	27	70	0.9	23.3	13.9	35.6	27.8	13.1	23.9	6.9	0	6.9	6	4
Yellow	AS	Tientsin	37	771	15	0.6	-8.9	32.2	22.8	31.7	53.3	19.3	0.3	19.1	2	2
Zambezi	AF	Zomba	16	1331	160	22.2	11.7	26.7	18.3	5.6	134.4	30.7	0.5	30.2	8	6

[a] AF = Africa; AS = Asia; AU = Australia; EU = Europe; NA = North America; SA = South America
[b] Winter = January in northern hemisphere, July in southern hemisphere; vice versa in summer
[c] Estimated from map