(*Sceloporus undulatus*) eggs exposed to simulated flood conditions. J. Herpetol. 26:338-341.

HINES, T. C., M. J. FOGARTY, AND L. C. CHAPPEL. 1968. Alligator research in Florida: a progress report. Proc. S. E. Assoc. Game Fish Comm. 22:166-180.

JOANEN, T. 1969. Nesting ecology of alligators in Louisiana. Proc. S. E. Assoc. Fish Game Comm. 23: 141-151.

———, L. M. MCNEASE, AND G. PERRY. 1977. Effects of simulated flooding on alligator eggs. Proc. S. E. Assoc. Fish Game Comm. 31:33-35.

KAM, Y.-C., AND R. A. ACKERMAN. 1990. The effect of incubation media on the water exchange of snapping turtle (*Chelydra serpentina*) eggs and hatchlings. J. Comp. Physiol. B 160:317-324.

KRAEMER, J. E., AND R. BELL. 1980. Rain-induced mortality of eggs and hatchlings of loggerhead sea turtle (*Caretta caretta*) on the Georgia coast. Herpetologica 36:72-77.

KUSHLAN, J. A., AND T. JACOBSEN. 1990. Environmental variability and the reproductive success of Everglades alligators. J. Herpetol. 24:176-184.

LUTZ, P. L., T. B. BENTLEY, K. E. HARRISON, AND D. S. MARSZALEK. 1980. Oxygen and water vapour conductance in the shell and shell membrane of the American crocodile egg. Comp. Biochem. Physiol. 66A:335-338.

MAGNUSSON, W. E. 1982. Mortality of eggs of the crocodile *Crocodylus porosus* in northern Australia. J. Herpetol. 16:121-130.

PACKARD, G. C., AND M. J. PACKARD. 1984. Coupling of physiology of embryonic turtles to the hydric environment. *In* R. S. Seymour (ed.), Respiration and Metabolism of Embryonic Vertebrates, pp. 99-119. Junk, Dordrecht, The Netherlands.

———, AND ———. 1988. The physiological ecology of reptilian egg and embryo. *In* C. Gans and R. B. Huey (eds.), Biology of the Reptilia, Vol 16. Ecology B, pp. 81-165. Alan R. Liss, Inc., New York.

PACKARD, M. J., G. C. PACKARD, AND T. J. BOARDMAN. 1980. Water balance of the eggs of a desert lizard (*Callisaurus draconoides*). Can. J. Zool. 58:2051-2058.

———, ———, AND ———. 1982. Structure of eggshells and water relations of reptilian eggs. Herpetologica 38:136-155.

PLUMMER, M. V. 1976. Some aspects of nesting success in the turtle, *Trionyx muticus*. Herpetologica 32:353-359.

TRACY, C. R. 1980. Water relations of parchment-shelled lizard (*Sceloporus undulatus*) eggs. Copeia 1980:478-482.

VLECK, D. 1987. Measurement of O_2 consumption, CO_2 production, and water vapor production in a closed system. J. Appl. Physiol. 62:2103-2106.

WEBB, G. J. W., H. MESSEL, AND W. E. MAGNUSSON. 1977. The nesting of *Crocodylus porosus* in Arnhem Land, northern Australia. Copeia 1977:238-249.

YNTEMA, C. L. 1968. A series of stages in the embryonic development of *Chelydra serpentina*. J. Morphol. 125:219-251.

Accepted: 11 January 1994.

Journal of Herpetology, Vol. 28, No. 2, pp. 178-187, 1994

Variation in East Asian Turtles of the Genus *Mauremys* (Bataguridae; Testudines)

JOHN B. IVERSON[1] AND WILLIAM P. MCCORD[2]

[1]*Department of Biology, Earlham College, Richmond, Indiana 47374, USA, and*
[2]*East Fishkill Animal Hospital, Hopewell Junction, New York 12533, USA*

ABSTRACT.—Morphometric variation in populations of East Asian *Mauremys* was evaluated with discriminant function and cluster analysis. *M. iversoni* is the most distinctive member of the group, although specimens from Guizhou Prov., China originally assigned to that taxon may represent an undescribed species. *Mauremys* (formerly *Annamemys*) *annamensis* is a morphometrically distinct species. *Annamemys grochovskiae* is a synonym of *M. mutica* (not *M. annamensis*). *Mauremys guangxiensis* is apparently a composite species; the holotype is apparently *M. iversoni* and the paratype is *M. mutica*.

Although there has been considerable confusion about the content of the Eurasian batagurid turtle genus *Mauremys* (e.g., see McDowell, 1964), with one major exception there now seems to be a consensus about its content (Bickham, 1975; Merkle, 1975; Ernst and Barbour, 1989) and monophyly (Sites et al., 1984; Hirayama, 1985). In addition, the taxonomic status of most of the included species has also recently been studied (Busack and Ernst, 1980; Iverson and McCord, 1989; Pritchard and McCord, 1991). However, the relationship of *Annamemys an-*

namensis (Siebenrock, 1903) to the genus *Mauremys* remains controversial.

Originally described as *Cyclemys annamensis* by Siebenrock (1903) on the basis of a juvenile specimen from Vietnam in the Vienna Museum (NMW), this form was later redescribed (as *A. merkleni*) by Bourret (1939) on the basis of eight specimens from Vietnam and placed in his new genus *Annamemys*. Bourret's (1939, 1941) primary diagnostic feature of this genus was the presence of massive axillary buttresses in contact with the first ribs. Savage (1953) subsequently demonstrated that *merkleni* and *annamensis* were synonymous, and McDowell (1964) then suggested that the condition of the axillary buttresses in *Annamemys* was not different from that in *Mauremys mutica* (Cantor, 1842). McDowell (1964) even recommended synonymizing *annamensis* with *M. mutica*. In addition, Iverson and McCord (1989) alluded to extensive variation in pigment patterns in *M. mutica*, and noted that its coloration in northern Vietnam approaches that of *A. annamensis*. However, presumably because McDowell's (1964) recommendation was based only on Bourret's figures (1939, 1941), and because skeletal material was not available to most subsequent authors (e.g., Hirayama, 1985), the genus *Annamemys* continues to be recognized by most authors (e.g., Ernst and Barbour, 1989; Iverson, 1992; but see Wermuth and Mertens, 1977:50).

Another problem concerns the identity of *Annamemys grochovskiae* Van Tien (1957), also from Vietnam. This taxon has not been discussed since its description, in which it was described as "possible to confuse . . . with *Clemmys mutica* Cantor" and "intermediate between *Annamemys* and *Clemmys* [*mutica*], but having more in common with *Annamemys* [*annamensis*]" (translated from the Russian). Unfortunately, it is not known if the holotype (presumably originally in the Hanoi University Zoological Laboratory) still exists.

More recently, Pritchard and McCord (1991) described the very distinctive *Mauremys iversoni* from Fujian province in southeastern China. However, the authors tentatively included several similar specimens from Guizhou province (over 1000 km to the west at an altitude of about 1250 m, which is over 750 m higher than any other East Asian *Mauremys* locality). The status of the Guizhou population clearly needs clarification.

Finally, in 1992 Qin [=Cen] described "*Clemmys*" *guangxiensis* based on two specimens purchased in Nanning, Guangxi province, China. However, photographs of the types provided to me by the author suggested that it might be a composite of *M. iversoni* and *M. mutica*. In order to clarify the systematic relationships of each of these Asian turtles allied to the genus *Mauremys*, we conducted this morphometric study.

MATERIALS AND METHODS

Shell and scute measurements (to the nearest mm) were recorded from all possible museum, pet trade, and figured specimens (see Specimens examined), representing 16 populations (Fig. 1): *Annamemys annamensis* (A; Vietnam), *Mauremys c. caspica* (C; Asia Minor), *M. c. rivulata* (U; southern Europe), *M. guangxiensis* (X; paratype, but measurements only from photograph taken perpendicular to the plastral midline), *M. iversoni* (I; Fujian Prov., China), *M. "iversoni"* (F; Guizhou Prov., China), *M. japonica* (J; Japan), *M. leprosa* (L; southwestern Europe and northwestern Africa), and eight populations of *M. mutica* [southern Ryukyu islands (R), Taiwan (T), Lower Yangzte basin (Y), eastern Guangdong Province (G), Si River basin (S), Hainan Island (H), between the Si River and Vietnam (B), and northern Vietnam (V).

Measurements included maximum (not midline) carapace length (CL), maximum carapace width (CW), maximum carapace height (CH), maximum (not midline) plastron length (PL), maximum (not midline) length of the plastral hindlobe from the interabdomino-interfemoral junction to a line across the posterior ends of the anal scutes (HL), plastral forelobe width at the level of the junction of the humero-pectoral seam and the plastral margin (PWA), anterior plastral hindlobe width at the level of the junction of the abdomino-femoral seam and the plastral margin (PWC), posterior plastral hindlobe width at the level of the junction of the femoro-anal seam and the plastral margin (PWD), right bridge length from axilla to inguinal pocket (BL), maximum ventral width across gular scutes (GW), maximum (not midline) length of right gular scute (GL), and lengths of right interhumeral (IH), interpectoral (IP), interabdominal (IAB), interfemoral (IF), and interanal (IAN) seams. Only subadult or adult specimens (>93 mm CL) were included in analyses. Because of sexual dimorphism in several characters, females and males were analyzed separately. Turtles that could not be sexed externally with certainty (e.g., articulated shells and subadults) were assigned a sex by within-species male versus female discriminant function analysis (DFA) with the questionable specimens as unknowns (i.e., classified a posteriori). The data were analyzed at three levels: (1) including all populations listed above; (2) including only the East Asian populations (i.e., excluding *M. c. caspica*, *M. c. rivulata*, and *M.*

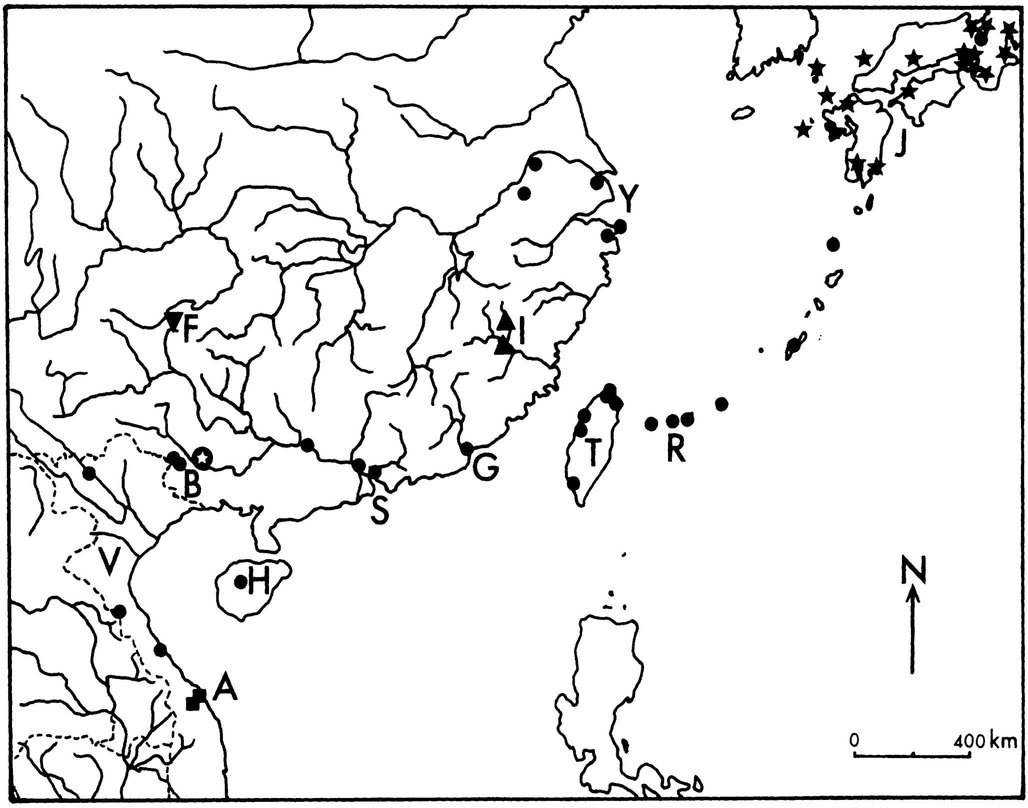

FIG. 1. Distribution of *Mauremys* in east Asia: *M. annamensis* (squares), *M. iversoni* (triangles), Guizhou *M. "iversoni"* (inverted triangle), *M. "guangxiensis"* (star in circle), *M. japonica* (stars), and *M. mutica* (solid dots). Capital letters mark population codes noted in text.

leprosa); and (3) including only populations of *M. mutica*.

Each subset of data was standardized for body size by regression against carapace length (see McCord and Iverson, 1991 for details); the 15 residuals were then submitted to DFA and UPGMA cluster analysis with SPSS software (SPSS, Inc., 1983). ANOVA and pairwise population comparisons for the residuals of each variable were made with Fisher's (protected) least significant difference (PLSD) test with STATVIEW software (Feldman et al., 1987). When only a single specimen of a given sex was available for analysis, that analysis was run twice, first with that specimen included in the DF model and second with that specimen excluded from the model but classified a posteriori (i.e., included as unknowns). Because data for *Annamemys grochovskiae* and *Mauremys guangxiensis* were only available from a figure and photographs, respectively, they were only run as unknowns in analyses.

RESULTS

The discriminant function analysis (DFA) of all populations (Fig. 2) demonstrates that *M. iversoni* (Fujian population only) is morphometrically one of the most distinctive in the genus (see also Figs. 3 and 4 in Pritchard and McCord, 1991). It also suggests that the Guizhou population of *M. "iversoni"* differs considerably from topotypic *M. iversoni*; however, this could be an artifact of having data from only a single female Guizhou specimen available for this analysis. *M. japonica* is shown to be similar to *M. leprosa*, but distinct from other East Asian forms. *Annamemys annamensis* is more divergent from *M. mutica* in the overall female analysis than in that for the males, only slightly overlapping populations of *M. mutica* in the latter analysis. Most of the populations of *M. mutica* cluster together; however, the Ryukyu population is somewhat divergent.

The DFA of only East Asian *Mauremys* (Fig. 3) again confirmed the distinctiveness of *M. iversoni, M. japonica, A. annamensis*, and the single female Guizhou specimen of supposed *M. "iversoni."* The latter was found to be equally divergent when the DFA was rerun with that specimen as an unknown. The Ryukyu population is also again demonstrated to be the most divergent among populations of *M. mutica*, and

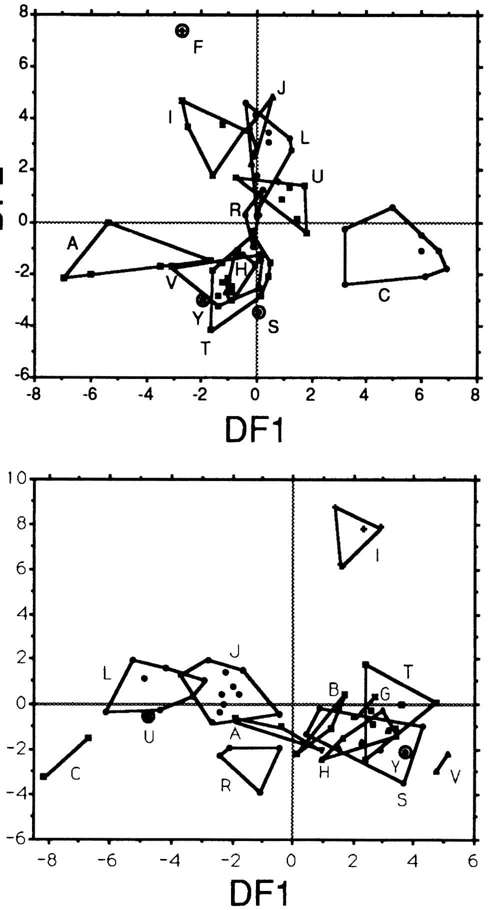

FIG. 2. Discriminant plots for populations of female (top) and male (bottom) *Mauremys*: *M. annamensis* (A), *M. c. caspica* (C), *M. c. rivulata* (U), *M. iversoni* (I), *M. "iversoni"* (F; Guizhou Prov.), *M. japonica* (J), *M. leprosa* (L), and eight populations of *M. mutica* [Ryukyu islands (R), Taiwan (T), Lower Yangzte basin (Y), eastern Guangdong Province (G), Si River basin (S), Hainan Island (H), between the Si River and Vietnam (B), and northern Vietnam (V). First axis accounts for 30.0 and 41.4% of the total variation, respectively; second axis, 29.7 and 26.8%, respectively.

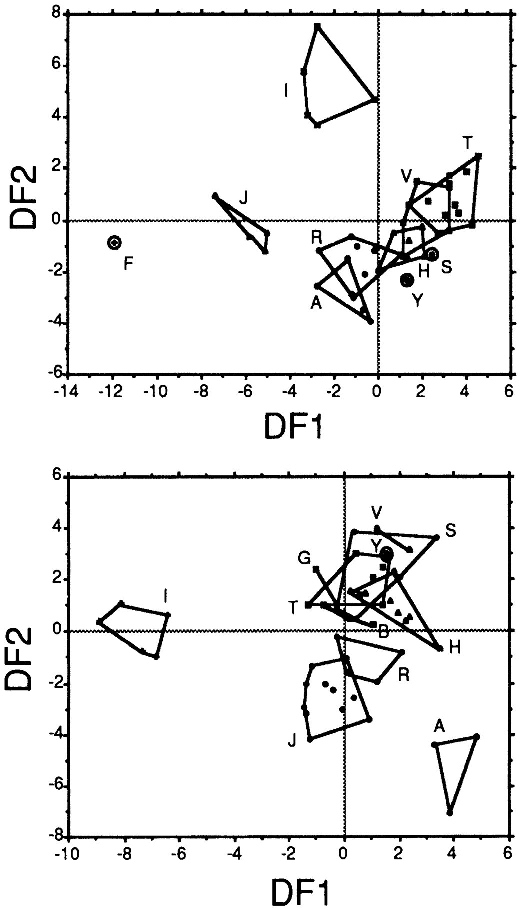

FIG. 3. Discriminant plots for populations of female (top) and male (bottom) East Asian *Mauremys* (symbols as in Fig. 2). First axis accounts for 45.2 and 39.7% of the total variation, respectively; second axis, 20.0 and 26.5%, respectively.

indeed is somewhat intermediate morphologically (and geographically!) between other populations of the latter and *M. japonica*.

UPGMA cluster analysis of male East Asian *Mauremys* placed specimens of *A. annamensis* in the most distinct outgroup, followed by specimens of *M. iversoni* and then of *M. japonica* as the next most divergent outgroups, respectively. All remaining populations (*M. mutica*) clustered in no identifiable geographic pattern. Clustering patterns were much less clear in the same analysis for females. Although there was a tendency for individual specimens of *A. annamensis*, *M. japonica*, and *M. iversoni* to be in the most divergent outgroups, for none of these taxa did all specimens cluster together.

The final DFAs (Fig. 4) of only populations of *M. mutica* suffered from small samples for one or both sexes from some populations (e.g., the lower Yangtze Basin for both sexes and the Si basin for females), but they nevertheless again suggested that Ryukyu specimens are distinct. For the first time, they also suggested that male Vietnamese *M. mutica* might be morphometrically distinct from other populations, but that female Vietnamese specimens are not. However, cluster analyses of female and male *M. mutica* revealed absolutely no pattern of clustering by population. For example, terminal specimen pairs were from different populations in eight of eleven cases in both the female and male analyses. ANOVAs of the residuals for males and females of populations of *M. mutica* (Table 1) suggested that the Ryukyu population

Table 1. Results of ANOVAs for males and females of populations (codes in text) of *Mauremys mutica* for characters standardized by regression against CL. All significant differences (at 5% by Fisher's protected least significant difference) between populations are listed. Note that the Ryukyu (R) population is the most consistently different population.

	Female (N = 32)		Male (N = 32)	
Residual	*P*	signif. differences	*P*	significant differences
CW	0.16		0.76	
SH	0.05	R vs. T, H, V	0.007	R vs. T, H, Y, V; B vs. T, H, V; S vs. V
PL	0.40		0.50	
HL	0.31		0.11	
PWA	0.97		0.03	R vs. T; V vs. T, H, G, S
PWC	0.02	R vs. T, H, V	0.32	
PWD	0.44		0.43	
BL	0.58		0.008	R vs. T, H, V; T vs. S, B
GW	0.70		0.11	
GL	0.04	R vs. H; H vs. S, V	0.17	
IH	0.36		0.05	R vs. T, Y, G, S, V
IP	0.66		0.07	S vs. T, H, G
IAB	0.53		0.59	
IF	0.99		0.29	
IAN	0.10	R vs. H, S	0.09	H vs. T, G, B; Y vs. B

was the most distinctive, but like the Asian male DFA, also suggested that males from Vietnam were somewhat divergent.

Discussion

The results indicate that *Mauremys iversoni* is morphometrically the most distinctive member of the genus in East Asia (see also Pritchard and McCord, 1991), followed by *M. japonica* (see also Table 2). They also confirm that *A. annamensis* is a distinct species, most similar to *M. mutica.* Since the characters originally used to diagnose the genus *Annamemys* (see Introduction) are shared by *Mauremys,* the former should be considered a junior synonym of the latter. However, despite their similarities, *M. annamensis* differs from *M. mutica* in its larger size (at least 285 mm versus at least 188 mm maximum CL), its female-dominated sexual size dimorphism (male-dominated or lacking in most *mutica* populations), its boldly striped head and neck (including a light yellow stripe over the eye, not found in *M. mutica;* Fig. 5), its moderately tricarinate carapace (weakly tricarinate to smooth in most *M. mutica*), its wider carapace and longer bridge, its narrower and longer gular scutes, its shorter interhumeral seam, and its longer interpectoral seam. Sympatry of the two species has not yet been established; their known ranges are separated by about 200 km in central Vietnam (Fig. 1).

Because the holotype of *Annamemys grochovskiae* Van Tien (1957) could not be located, comparisons of that form with *M. annamensis* and *M. mutica* were made based only on the original description and figures. Van Tien's (1957) diagnosis includes several characters that vary considerably even within *M. annamensis* and *M. mutica* (e.g., the juxtaposition of the anterior plastral seams and the underlying sutures; see Nakamura, 1934). However, several characters do appear to be diagnostic for *M. mutica.* First, Van Tien describes a "small yellowish sideband above the temporal region [that] becomes inconspicuous in the middle of the neck." This condition applies to Vietnamese *M. mutica,* but not to *M. annamensis* (Fig. 5). Second, the description and figure of the holotype show that Van Tien's turtle had a relatively narrow carapace, a relatively short intergular seam, and a relatively long interhumeral seam, each characteristic of *M. mutica* (Fig. 6). Finally, measurements were taken from the specimen in Fig. 1d in Van Tien (1957), standardized by regression against measured carapace length, and the residuals included as unknowns in a DFA of Vietnamese *M. mutica* versus Vietnamese *M. annamensis.* That analysis revealed no overlap in the latter two taxa in phenetic space and classified *M. grochovskiae* as *M. mutica* with a probability of 100%. In conclusion, until the holotype is located for positive identification, *A. grochovskiae* should be considered a synonym of *M. mutica.*

As discussed in the Introduction, *M. guangxiensis* (Qin, 1992) seems to represent a composite of *M. iversoni* and *M. mutica.* From a photograph of the holotype in life provided by Qin, it is clear that its head markings are identical to those of *M. iversoni,* which are unique among all known *Mauremys.* In addition, a DFA of the residuals of all Chinese *Mauremys* populations with those generated from measurements taken from a photograph of the plastron of the para-

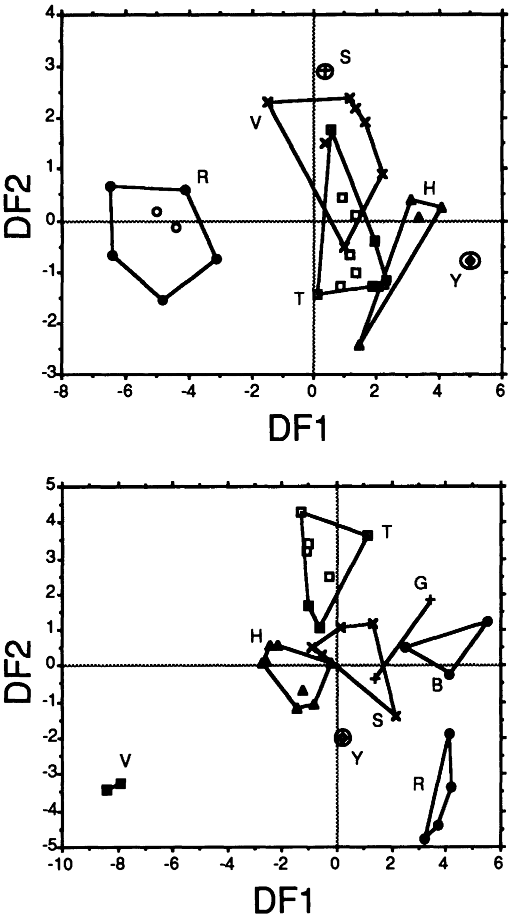

FIG. 4. Discriminant plots of first two canonical axes for populations of female (top) and male (bottom) *Mauremys* (symbols as in Fig. 2). First axis accounts for 88.0 and 48.2% of the total variation, respectively; second axis, 8.5 and 23.6%, respectively. Note that because only single specimens were available for populations S and Y, they were classified a posteriori (see Methods).

type provided by Qin classified that specimen with the Hainan Island population of *Mauremys mutica* with a probability of 100%. There seems to be little doubt that the paratype represents *M. mutica*. Both types were purchased in Nanning, Guangxi Province, but neither likely were collected there.

The Guizhou specimen is most clearly related to *M. iversoni* based on its color pattern (see also Pritchard and McCord, 1991), but it differs from the latter in its wider plastral hindlobe (PWC and PWD) and its relatively longer interabdominal seam. Only the study of additional material with confirmed locality data can resolve the taxonomic status of this population.

There is considerable geographic variation in head and skin coloration within *M. mutica* (Fig.

TABLE 2. Summary of taxonomically useful character ratios for distinguishing adult and subadult East Asian species of the genus *Mauremys*. Character abbreviations are carapace length (CL in mm), carapace width (CW), maximum plastron length (PL), anterior width of plastral hindlobe (PWC), bridge length (BL), gular width (GW), gular length (GL), interhumeral seam length (IH), interpectoral seam length (IP), interabdominal seam length (IAB), interfemoral seam length (IF), and interanal seam length (IAN). Values are means for each sex for each taxon (except maximum CL appears in parentheses).

Taxon	Sex	N	CL (max)	CW/CL	PL/CL	PWC/CL	BL/CL	GW/CL	GL/CL	IH/CL	IP/CL	IAB/CL	IF/CL	IAN/CL
M. iversoni	M	5	160.9 (194)	0.665	0.914	0.449	0.330	0.190	0.137	0.074	0.206	0.192	0.141	0.128
	F	5	174.4 (193)	0.718	0.935	0.487	0.353	0.194	0.141	0.079	0.212	0.198	0.138	0.140
M. "iversoni"	F	1	129.3 (—)	0.774	0.947	0.510	0.333	0.189	0.158	0.054	0.179	0.236	0.107	0.160
M. japonica	M	11	123.1 (174)	0.691	0.915	0.433	0.320	0.230	0.126	0.075	0.164	0.227	0.166	0.094
	F	4	153.6 (184)	0.689	0.969	0.517	0.356	0.212	0.108	0.104	0.173	0.234	0.150	0.129
M. annamensis	M	4	168.7 (188)	0.781	0.889	0.469	0.340	0.177	0.130	0.089	0.165	0.180	0.182	0.087
	F	6	191.1 (285)	0.762	0.915	0.463	0.368	0.172	0.139	0.083	0.187	0.185	0.173	0.097
M. mutica (non-Ryukyu)	M	28	141.6 (187)	0.703	0.897	0.425	0.321	0.217	0.111	0.131	0.152	0.182	0.178	0.093
	F	25	143.9 (187)	0.708	0.918	0.449	0.340	0.213	0.114	0.128	0.159	0.188	0.178	0.094
M. mutica (Ryukyu)	M	4	156.0 (179)	0.690	0.872	0.426	0.293	0.217	0.125	0.101	0.140	0.189	0.175	0.093
	F	7	130.3 (149)	0.744	0.924	0.480	0.332	0.226	0.123	0.118	0.144	0.198	0.181	0.103

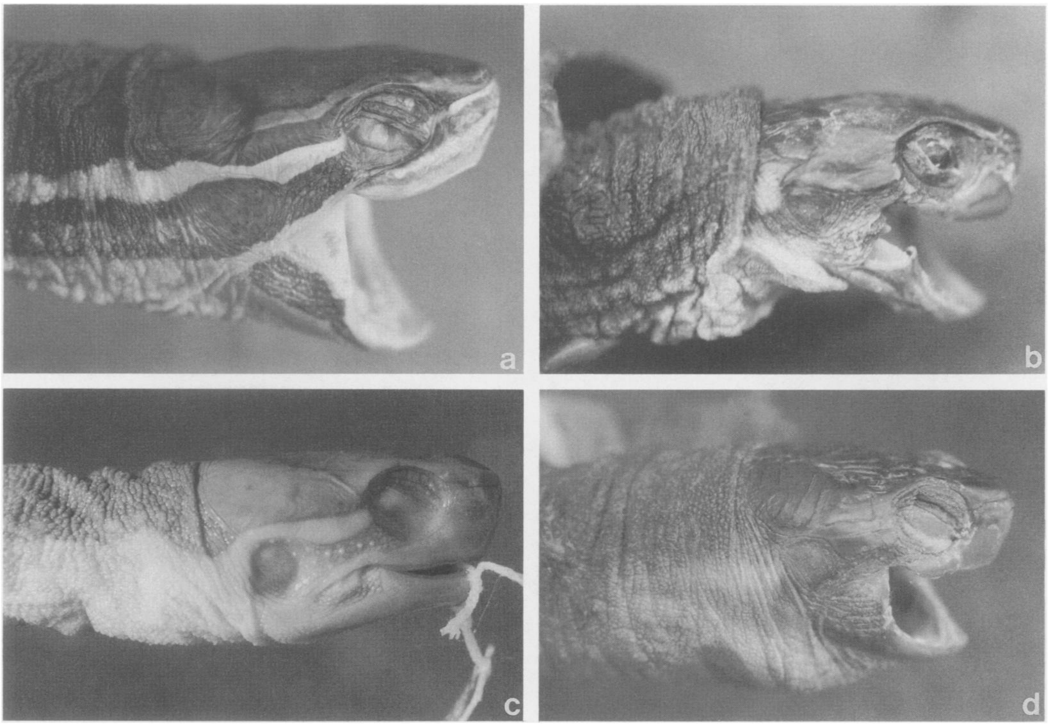

FIG. 5. Head patterns of adult female Asian *Mauremys*: a) *M. annamensis* (171 mm CL; Vietnam; UF 87179); b) *M. mutica* (158 mm CL; Vietnam; UF 87133); c) *M. mutica*, (148 mm CL; Taiwan; FMNH 127181); and d) *M. mutica* (149 mm CL; Ryukyu Islands; UF 87132).

5), most apparently clinal. Northeastern populations are light grayish-yellow in color with almost no evidence of a temporal head stripe, whereas central populations (e.g., in southeastern China) have a fairly obvious yellow temporal stripe and the skin suffused with yellow pigment. However, southwestern populations have a much darker head and skin, and the temporal stripe is very bold, being bright yellow and bordered by thin black lines. In general, there is also more dark plastral pigment in southwestern populations as well (Fig. 6; see also Iverson and McCord, 1989). On the contrary, morphometric variation within *M. mutica* is not great (Table 1); however, the discriminant analyses and ANOVAs both suggested that among the populations of *M. mutica,* that from the Ryukyu islands is the most divergent. However, this analysis did not include adequate samples of several populations of *M. mutica,* particularly those in northeastern China, the northern Ryukyus, and at Kyoto in central Japan (Nakamura, 1934; Hikida et al., 1992). Thus, the Ryukyu population may deserve taxonomic status, but a more complete analysis of variation within *M. mutica* (in progress by Ota, Yasukawa, and Iverson) will be necessary to settle the issue.

Although a strict cladistic analysis of the entire genus *Mauremys* is not yet possible, the phenetic relationships among the East Asian species suggest a preliminary phylogenetic hypothesis for the Asian clade (Fig. 7). Studies of variation in the mitochondrial genome of this genus now in progress will test this hypothesis.

In an attempt to understand the pattern of evolution in the continuous characters measured in this study, mean values of each character that varied significantly across the Asian species of *Mauremys* were superimposed on the phylogeny (males and females separately) and significant shifts in character values (from Fisher's PLSD) were noted. Those changes that were common to both males and females are indicated on the phylogeny in Fig. 7. That process suggested two patterns that may have functional significance: (1) that an increase in relative interpectoral seam length may be correlated with a decrease in relative interhumeral seam length, and (2) that increases in carapace length, relative carapace width, and relative bridge length may all be correlated. The tradeoff in lengths of the interpectoral and interhumeral seams may be related to the importance of the degree of overlap of the pectoral scutes onto

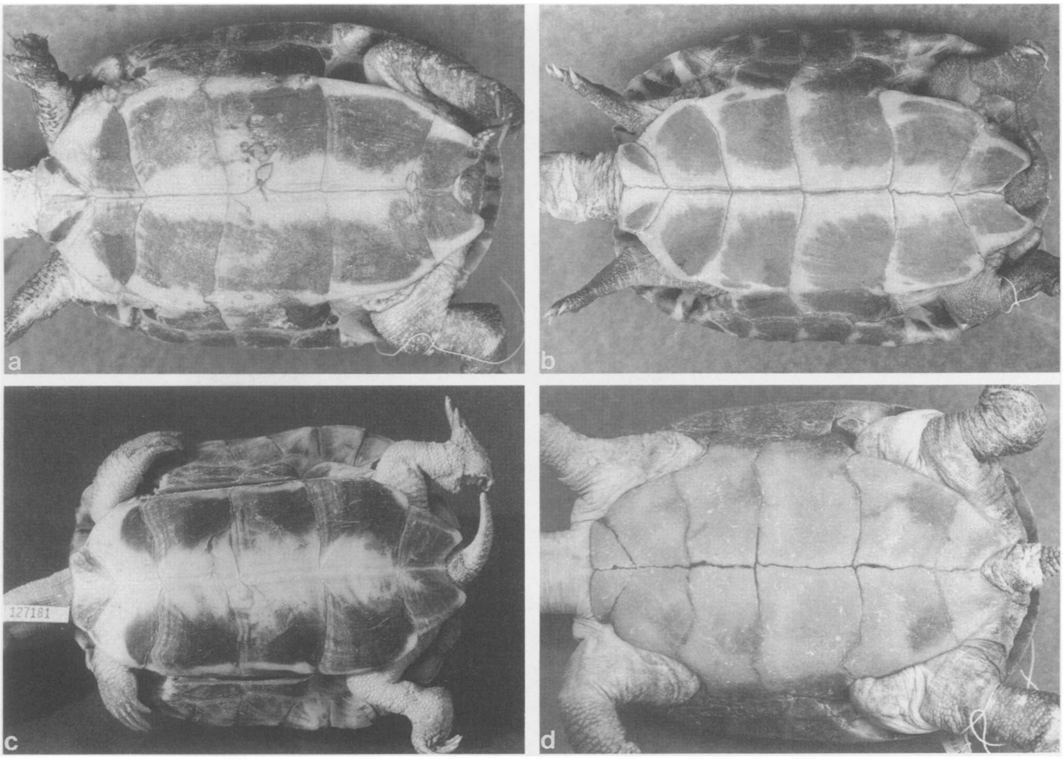

FIG. 6. Plastral patterns of adult female Asian *Mauremys*: same specimens as in Fig. 5.

the entoplastron, greater overlap presumably providing greater strength to the plastral forelobe. Similarly, a larger, broader shell (i.e., a wider arch) may require a longer bridge to provide sufficient buttressing to reduce the possibility of being crushed and swallowed by large predators. Indeed, the only species of *Mauremys* which exhibits these last three characters (*M.*

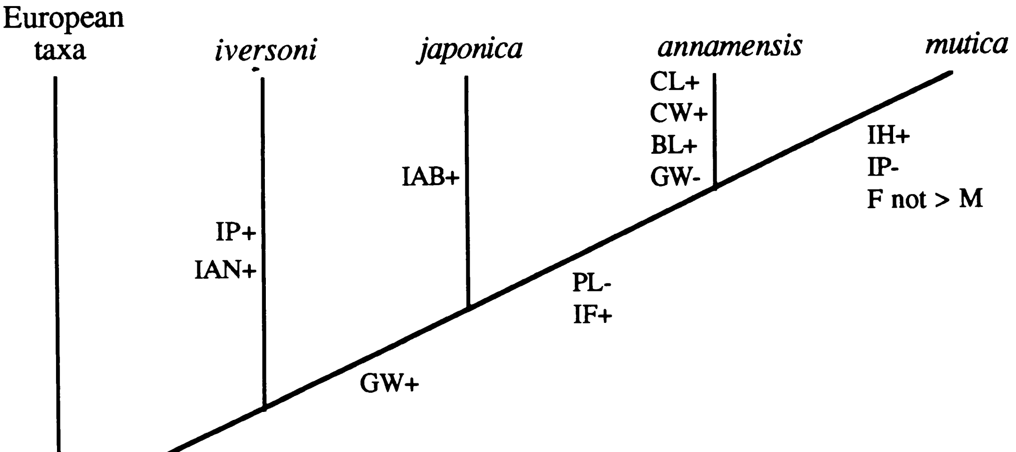

FIG. 7. Preliminary phylogeny for the East Asian members of the genus *Mauremys* based on phenetic relationships. Significant character shifts are indicated (+ = an increase in relative size; − = a decrease; M not >F indicates no female-dominated size dimorphism).

annamensis) is the only one whose range is wholly within that of a crocodile (*Crocodylus porosus*; Ross, 1989).

Acknowledgments.—This study would not have been possible without the generous loan of specimens by the American Museum of Natural History (AMNH), the British Museum of Natural History (BMNH), the California Academy of Sciences (CAS), the Field Museum of Natural History (FMNH), the University of Kansas (KU), the Paris Museum (MNHN), the Museum of Vertebrate Zoology at Berkeley (MVZ), the Vienna Museum (NMW), the University of Florida (UF), the University of Michigan Museum of Zoology (UMMZ), the United States National Museum (USNM), W. P. McCord (WPM), the Hamburg Museum (ZMH), M. A. Ewert (Indiana Univ.), and M. Goode (Columbus Zoo). We especially thank Satoshi Tanaka for securing the UF Ryukyu specimens. Jianqiang Cen of the Shanghai Museum (SNHM) and F. Tiedemann of the Vienna Museum (NMW) provided photographs of the types of *M. guangxiensis* and *M. annamensis*, respectively. Cathy Flick and Leo Chang assisted with translations (Russian and Chinese, respectively). The comments of K. Adler, R. Bour, J. R. Buskirk, J. Cen, and H. Ota on an early draft of the manuscript are greatly appreciated. Financial support was provided by the Earlham College Professional Development Fund, the Joseph Moore Museum of Natural History, and Iverson's family.

LITERATURE CITED

BICKHAM, J. W. 1975. A cytosystematic study of turtles in the genera *Clemmys, Mauremys,* and *Sacalia.* Herpetologica 31:198–204.

BOURRET, R. 1939. Notes herpétologiques sur l'Indochine Française, XVIII. Reptiles et batraciens recus au Laboratoire des Science Naturelles de l'Universite au cours de l'annee 1939. Descriptions de quatre especies et d'une variete nouvelles. Bull. Gen. Instr. Publ., Hanoi 1939:5–39.

———. 1941. Les Tortues de l'Indochine. Inst. Océanograph. l'Indochine, Hanoi. 235 pp.

BUSACK, S. D., AND C. H. ERNST. 1980. Variation in Mediterranean populations of *Mauremys* Gray 1869 (Reptilia, Testudines, Emydidae). Ann. Carnegie Mus. Nat. Hist. 49:251–264.

CANTOR, T. 1842. General features of Chusan, with remarks on the flora and fauna of that island [Part 3]. Ann. Mag. Nat. Hist. London [Ser. 1] 9:481–493.

ERNST, C. H., AND R. W. BARBOUR. 1989. Turtles of the World. Smithsonian Inst. Press, Washington, D.C. 313 pp.

FELDMAN, D. S., J. GAGNON, R. HOFMANN, AND J. SIMPSON. 1987. Statview II. Abacus Concepts, Berkeley, California. 247 pp.

HIKIDA, T., H. OTA, AND M. TOYAMA. 1992. Herpetofauna of an encounter zone of Oriental and Palearctic elements: amphibians and reptiles of the Tokara Group and adjacent islands in the northern Ryukyus, Japan. Biol. Mag. (Okinawa) 30:29–43.

HIRAYAMA, R. 1985. Cladistic analysis of batagurine turtles (Batagurinae: Emydidae: Testudinoidea); a preliminary result. Stud. Geol. Salmanticensia Vol. Esp. 1. Stud. Paleonchelonolog. I. 1984:141–157.

IVERSON, J. B. 1992. A Revised Checklist with Distribution Maps of the Turtles of the World. Iverson Publishing, Richmond, Indiana. 363 pp.

———, AND W. P. MCCORD. 1989. The proper taxonomic allocations of *Emys nigricans* Gray, *Emys muticus* Cantor, and *Geoclemys kwangtungensis* Pope. Amphibia-Reptilia 10:23–33.

MCCORD, W. P., AND J. B. IVERSON. 1991. A new box turtle of the genus *Cuora* (Testudines: Emydidae) with taxonomic notes and a key to the species. Herpetologica 47:407–420.

MCDOWELL, S. B. 1964. Partition of the genus *Clemmys* and related problems in the taxonomy of the aquatic Testudinidae. Proc. Zool. Soc. London 143: 239–279.

MERKLE, D. A. 1975. A taxonomic analysis of the *Clemmys* complex (Reptilia: Testudines) using starch gel electrophoresis. Herpetologica 31:162–166.

NAKAMURA, K. 1934. On *Clemmys mutica* (Cantor) with special reference to its variations and distributions. Annot. Zool. Japan 14:425–435.

PETZOLD, H. G. 1963. Über einige Schildkröten aus Nord-Vietnam im Tierpark Berlin. Senck. Biol. 44: 1–20.

PRITCHARD, P. C. H. 1979. Encyclopedia of Turtles. T. F. H. Publ., Inc. Neptune, New Jersey. 895 pp.

———, AND W. P. MCCORD. 1991. A new emydid turtle from China. Herpetologica 47:139–147.

QIN [=CEN], J. 1992. A new species of genus *Clemmys*: *C. guangxiensis. In* Y. Qian, E. Zhao, and K. Zhao (eds.), "1991" (atually 1992). Animal Science Research. A volume issued to celebrate the 90th birthday of Mangven L.-Y. Chang. pp. 60–62. China Forestry Press, Beijing (12)2:1–248.

ROSS, C. A. (ed.). 1989. Crocodiles and Alligators. Facts on File, New York. 248 pp.

SAVAGE, J. M. 1953. Remarks on the Indo-chinese turtle *Annamemys merkleni.* Ann. Mag. Nat. Hist. London 6:468–472.

SIEBENROCK, F. 1903. Schildkröten des östlichen Hinterindien. Sitz. Akad. Wiss. Wien. Math.-natur. Kl. 112:333–352.

SITES, J. W., J. W. BICKHAM, B. A. PYTEL, I. F. GREENBAUM, AND B. A. BATES. 1984. Biochemical characters and the reconstruction of turtle phylogenies: relationships among batagurine genera. Syst. Zool. 33:137–158.

SPSS, INC. 1983. SPSS^x User's Guide. McGraw-Hill, New York.

VAN TIEN, D. 1957. Rapport sur les recherches zoologiques dans la region de Vinh-Linh (Province de Quang-Tri, Centre Vietnam). Zoolog. Zhurn. 36: 1209–1216. [In Russian with French summary].

WERMUTH, H., AND R. MERTENS. 1977. Liste der rezenten Amphibien und Reptilien. Testudines, Crocodylia, Rhynchocephalia. Das Tierreich, Berlin 100:1–174.

Accepted: 14 January 1994.

APPENDIX 1

Specimens Examined

Mauremys annamensis: Vietnam (CAS-SU 9142 [syntype of *merkleni*]; Columbus Zoo live specimen [apparently the specimen photographed in Pritchard, 1979]; MNHN 1948-39 [syntype of *merkleni*]; NMW 23394 [holotype, photograph only, provided by Franz Tiedemann]; UF 87177-85; and WPM 1-7 [alive]). *M. c. caspica:* Iraq (FMNH 19708-09, 74949); Iran (FMNH 73495, 141619); Syria (FMNH 73494); and Turkey (FMNH 82663-66). *M. c. rivulata:* Greece (UMMZ 65472-78, 70191). *M. "guangxiensis":* China, Guangxi Prov. (SNHM 88701, holotype; and 88702, paratype; photographs only, provided by Jianqiang Cen). *M. iversoni:* China, Fujian Prov. (UF 71865-66; and WPM, 10 live specimens). *M. "iversoni":* China, Fuizhou Prov. (WPM, 1 live specimen). *M. japonica:* Japan (CAS-SU 15825-29, 16038, 26123, 26125-26; UF 49426; and USNM 9551, 34066-75). *M. leprosa:* Morocco (FMNH 199761-64, 197887-88); Portugal (KU 144273); Spain (CM 51038, 53367, 54682, 55331, 55501, 55675 [4 specimens]); and Tunisia (CM 54543). *M. mutica:* China, lower Yangtze basin (AMNH 31065; WPM, 1 live specimen); China, Guangdong Prov. (MVZ 23937-38); China, Si River basin (WPM, 9 live specimens); China, between Si River and Vietnam border (UF 87134-35; WPM, 3 live specimens); China, Hainan Island (AMNH 30154, 30157-60, 30164-66, 30168; BMNH 1929.7.3.5; FMNH 6588-90, 6592, 15905; and WPM, 3 live specimens); China, no further data (BMNH 1947.3.5.34 [holotype], 1987.1183]; Taiwan (AMNH 84519; BMNH 1922.16.5-7 [3 specimens]; and FMNH 127181-82, 127184, 127187, 127189-93, 127195, 127197-202); Vietnam, near China border (UF 87133; WPM, 8 live specimens; ZMH R00274 [photograph in Petzold, 1963]); and Japan, Ryukyu Islands (BMNH 1933.5.19.1-2 [2 specimens]; CAS-SU 21010-14, 26116-19; and UF 87131-32).

Journal of Herpetology, Vol. 28, No. 2, pp. 187-192, 1994

Foraging Activity and Diet of Four Sympatric Lizard Species in a Tropical Rainforest

THIERRY R. GASNIER, WILLIAM E. MAGNUSSON, AND ALBERTINA P. LIMA

Departamento de Ecologia, Instituto Nacional de Pesquisas da Amazônia,
Caixa Postal 478, 69011 Manaus AM, Brazil

ABSTRACT.—**Observations on the foraging activity and diets of four sympatric rainforest lizards were used to test previous generalizations based mainly on studies on lizards from arid areas. In contrast to lizards studied in arid areas, an ambush predator (*Uranoscodon superciliosa,* Iguanidae) eats more hidden and slow moving prey than the most active forager (*Kentropyx calcarata,* Teiidae). *Plica umbra* (Iguanidae), an ant specialist, has similar foraging intensity to *Anolis punctatus* (Iguanidae) and is more active than *U. superciliosa,* which are generalist insectivores. *Plica umbra* does not have the behavioral and morphological adaptations for myrmecophagy that commonly occur in desert lizards. *Uranoscodon superciliosa* also does not specialize on large prey, as predicted for extreme "sit-and-wait" lizards in tropical rainforests. Differences in the consequences of foraging mode for the diet of lizards between arid and forest areas may be affected by differences in the availability of prey and their distribution in the environment.**

The types of invertebrates present in the diets of diurnal lizards are generally related to the mean rates of movement of the species during their foraging activities (e.g., Andrews, 1979; Dunham, 1983; Huey and Pianka, 1981; Magnusson et al., 1985; Anderson and Karasov, 1988). In general, actively moving species in arid areas eat sedentary prey (e.g., insect larvae), unpredictably distributed and clumped prey (e.g., termites), or large and inaccessible prey (e.g., inactive scorpions), while less actively moving species eat more mobile prey (Pianka, 1970; Parker and Pianka, 1975; Huey and Pianka, 1981; Nagy et al., 1984; Magnusson et al., 1985; Toft, 1985; Anderson and Karasov, 1988). Lizard species that eat mainly ants are generally among the least active (Pianka and Parker, 1975; Whitford and Bryant, 1979).

The only generalization about the relationship between foraging activity and diet of lizards in tropical rainforest we are aware of is that of Andrews (1979). Based on observations of the iguanid *Corytophanes cristatus,* she suggested that extreme "sit-and-wait" behavior (ambush foraging strategy) is associated with a diet specialized on large prey items.