

Differential Headbob Displays toward Neighbors and Nonneighbors in the Territorial Lizard *Anolis sagrei*

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ABSTRACT.—Animals in territorial neighborhoods often show differential behavior toward different classes of conspecifics. We tested whether males of the lizard *Anolis sagrei* outside of their territorial neighborhoods differed in visual display behavior when matched with neighbors versus with nonneighbors. We captured nine dyads of neighbors and nine dyads of nonneighbors, placed each dyad on an artificial habitat patch in the field, and then observed display behavior for one hour. Dyads of neighbors exhibited a smaller proportion of bobbing headbob displays than did dyads of nonneighbors. The direction of this display difference is consistent with the hypothesis that neighbors were treated less aggressively than nonneighbors.

Many territorial animals live in neighborhoods that can be socially complex. Often territory owners behave differently toward different classes of individuals, such as neighbors, strangers, or subordinate floaters. For example, different levels of aggression may be shown toward different individuals (reviewed in Temeles, 1994). A common pattern of differential aggression is known as the “dear enemy phenomenon” (Fisher, 1954), in which less aggression is shown toward familiar individuals, at least in some contexts. However, territorial animals can also exhibit other patterns of differential behavior (Temeles, 1994), including cooperation with neighbors (Elfstrom, 1997).

For lizards, as well as most other organisms, we know little about what patterns of differential behavior occur and the causes of any patterns. However, a number of hypotheses have been postulated. One possibility is that different classes of individuals representing different levels of threat cause differential aggression. For example, an individual without a territory might attempt to take over space from the territory owner or disrupt social stability within the neighborhood and thereby be a greater threat to a territory owner than a neighbor (see Beletsky, 1992; Stamps, 1994; Temeles, 1994; Paterson, 2002). Another possibility is that differential aggression is caused by a territory owner having differing amounts of information about different individuals (Ydenburg et al., 1988). Animals often settle conflicts with a minimum of aggression when they know each other’s fighting ability and motivation (e.g., Maynard Smith and Parker, 1976; Matsuura and Kobayashi, 1998).

The ability to engage in such differential behavior may be constrained by the ability to recognize different classes of individuals. For example, in some species, more aggression is shown toward neighbors when they are in atypical locations (e.g., see Husak

and Fox, 2003). One possible reason for this is that neighbors may not be recognized as neighbors under such circumstances.

Here we report an experimental test of whether male Brown Anoles (*Anolis sagrei*) in a neutral arena can distinguish between two classes of conspecifics: neighbors and nonneighbors. During the breeding season, male *A. sagrei* occupy small home ranges of 5–25 m² and defend these areas as territories against other males, thereby creating an excellent system for studying territorial neighborhoods (see Schoener and Schoener, 1982; Tokarz, 1998; Paterson, 2002; McMann and Paterson, 2003a; Tokarz et al., 2003). Interactions among male *A. sagrei* are conducted primarily through exchanges of various headbob displays (Scott, 1984; McMann, 2000; McMann and Paterson, 2003a; Tokarz et al., 2003). Thus, we surmised that, if displays during dyadic interactions between neighbors differed from displays during dyadic interactions between nonneighbors, we would have sufficient evidence to conclude that male *A. sagrei* can distinguish neighbors from nonneighbors.

The frequency of headbob displays in this species seems to be strongly influenced by variation in weather conditions typically experienced during the breeding season (unpubl. data). However, two general forms of headbob displays, bobbing and nodding (see McMann, 2000), have different relative frequencies in different social contexts. Higher proportions of bobbing displays occur when lizards are outside the cores of established home ranges and when potential rivals are nearby (McMann, 2000; McMann and Paterson, 2003a). Bobbing displays also become relatively more frequent before acts of physical aggression such as attempts to bite an opponent (unpubl. data). Therefore, we used the proportion of headbob displays that were bobbing displays to test whether display behavior differed between neighbors and nonneighbors. This is a conservative test in the sense that a negative result would not rule out displays differing in other ways, nor would it rule out the possibility that lizards can distinguish neighbors from nonneighbors without behaving differently when with neighbors than with nonneighbors.

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TABLE 1. Characteristics of headbob displays given in neighbor dyads and nonneighbor dyads. Displays from both individuals with a dyad are pooled. Values are presented as mean and standard error ($N = 9$).

Variable	Neighbor dyads	Nonneighbor dyads
Proportion bobbing displays	0.03 \pm 0.02	0.19 \pm 0.06
Proportion with crests	0.04 \pm 0.04	0.29 \pm 0.11
Number per hour	26.7 \pm 6.1	51.7 \pm 7.4

MATERIALS AND METHODS

During June and July of 1998, we captured male *A. sagrei* in the vicinity of Miami, Florida, as needed for our study. Prior to capture, we ensured that all males displayed without being challenged by other males, making it more likely that captured males held territories before capture. Lizards that were initially seen < 2 m apart were classified as neighbors and lizards that were initially seen > 50 m apart were classified as nonneighbors. These categories are based on typical home-range sizes for this species (e.g., Schoener and Schoener, 1982). On a typical day, we captured two dyads of neighbors and five individual nonneighbors. After capture we transported each lizard to the laboratory at the University of Miami where we measured its mass and snout-vent length (SVL). Four nonneighbors were then assigned to two dyads of nonneighbors.

Because body size can affect interactions among male *A. sagrei* (Tokarz, 1985), we controlled for body size and body size differences within dyads by size-matching lizards in nonneighbor dyads with lizards in neighbor dyads. We did this by first recording the body mass of individuals in a neighbor dyad, then constructing a corresponding nonneighbor dyad from the available nonneighbors that were most similar in mass to each neighbor. To confirm whether we controlled for body size, we tested whether dyads of neighbors differed from dyads of nonneighbors in mean body mass, mean SVL, mass difference within a dyad, and SVL difference within a dyad. We tested each variable with either a *t*-test for unpaired data or with a Wilcoxon's two-sample test depending on whether the data met the assumptions for a *t*-test (Sokal and Rohlf, 1995). There were no significant differences between neighbors and nonneighbors in any of the measured traits (see Results).

Prior to trials, we held the lizards for 1–2 nights in separate cloth bags in separate plastic containers. After sunrise on the morning of a trial day, the first author released two dyads at a field site at Fairchild Tropical Gardens, Miami, Florida. Each dyad was placed on an artificial habitat patch similar to those used in other field studies of *A. sagrei* (McMann, 2000; McMann and Paterson, 2003b). Each patch contained a potted fig tree (*Ficus benjamina*) surrounded by vegetative debris (i.e., sticks, palm fronds) and created a suitable environment for *A. sagrei* (McMann, 2000). Each patch was about 1.5 m high, 2 m in diameter, and located on mowed grass at least 6 m from other patches or complex vegetation. Just before a trial, the patch was dismantled, and adult males were removed before it was reassembled. Females and juveniles were left on the patches to provide a natural context for territorial behavior. We

used coin tosses to determine which individual in a dyad would be placed in a patch first (within a few seconds of the second lizard) and to determine the color of each individual's identifying number. Each lizard's number was painted on its back using white, purple, or pink acrylic paint pens (Speedball Painters markers, Hunt Manufacturing Co., Statesville, NC). On successive trial days, we alternated whether a dyad of neighbors or nonneighbors was released first and whether neighbors or nonneighbors were placed on a specific patch.

After a dyad of lizards was placed on a patch the first author observed behavior for the following hour from a location approximately 5 m east of the patch. This species appears to be undisturbed by similar observation protocols (McMann and Paterson, 2003b) and because observations were carried out during the morning, the lizards were generally visible on the sunny eastern sides of patches. Once observations were completed on the first patch, the second dyad was similarly released and observed on the second patch.

For each dyad, we recorded the proportion of headbob displays that were bobbing displays. To provide a more general description of behavior, we also recorded the frequency of headbob displays and the proportion of headbob displays with crest erection. The erection of a dorso-nuchal crest occurs in highly escalated aggressive interactions among mature male anoles (Greenberg, 1977; Jenssen, 1979; Scott, 1984). Aggressive interactions in the field can also escalate to physical fighting (e.g., McMann, 2000), but physical fights were not observed in this study.

We analyzed data with PC-SAS (Rel. 8.2, Williams Baptist College, SAS Institute, Inc., Cary, NC, 2001) and considered an alpha of < 0.05 to be significant in all statistical tests. Comparisons between neighbors and nonneighbors were modeled as comparisons between unpaired populations of dyads. We tested whether the proportion of headbob displays that were nodding displays differed between neighbors and nonneighbors with a Wilcoxon's two-sample test (Sokal and Rohlf, 1995). We did not use other variables to test for a significant difference between treatments because (1) corrections for an experiment-wise error rate would have made multiple univariate tests overly conservative and (2) results of multivariate analyses can be difficult to interpret in terms of recognizable behavior patterns. However, we present descriptive data on the other behavioral variables in Table 1.

Although the difference was not statistically significant, neighbors and nonneighbors differed somewhat in the difference in mass of individuals comprising dyads (see Results). Therefore, we tested for a correlation between mass difference and the proportion of headbob displays that are bobbing displays with a Spearman Rank Correlation Analysis (Sokal and Rohlf, 1995).

RESULTS

Dyads of neighbors contained lizards that were similar in mean size to those of nonneighbors. There were no significant differences between neighbors and nonneighbors in body mass (neighbors = 5.57 \pm 0.27 g, nonneighbors = 5.54 \pm 0.28 g, $t_{16} = -0.08$, $P = 0.93$), SVL (neighbors = 56.6 \pm 0.8 mm, nonneighbors = 56.7 \pm 0.7 mm, $t_{16} = 0.15$, $P = 0.88$), mass differences

within dyads (neighbors = 0.51 ± 0.12 g, nonneighbors = 0.74 ± 0.11 g, $z = 1.50$, $P = 0.13$) and SVL differences within dyads (neighbors = 2.28 ± 0.43 mm, nonneighbors = 2.22 ± 0.62 mm, $z = 0.04$, $P = 0.96$).

There was significant variation between neighbors and nonneighbors in the visual displays exhibited by dyads (Table 1). The nine dyads of neighbors had a lower proportion of headbob displays that were bobbing displays than did the nine dyads comprised of individuals that were nonneighbors ($z = 2.26$, $P = 0.024$). There also appeared to be other display differences between neighbors and nonneighbors, although we did not test whether the differences were statistically significant. For example, the mean proportion of headbob displays accompanied by crest erection among neighbors was less than one fifth of that among nonneighbors (Table 1). Similarly, the mean number of headbob displays among neighbors was about half the mean number among nonneighbors (Table 1).

The difference in mass of individuals comprising dyads was not correlated with the proportion of bobbing displays among neighbors ($r = 0.32$, $P = 0.40$), nonneighbors ($r = 0.03$, $P = 0.94$), or both treatment groups pooled ($r = 0.15$, $P = 0.56$). Thus, it is unlikely that body size affected our inferences about treatment effects.

DISCUSSION

The current study indicates that, when male *A. sagrei* are removed from their territorial neighborhoods, they behave differently when with former neighbors than they do when with nonneighbors. It is important to note that, during our study, lizards within a dyad were generally within a meter of each other, whereas free-ranging males often display when rival lizards are farther away. Short distance interactions can differ from long distance interactions in how headbob displays vary between social contexts (McMann, 2000). However, our study indicates that at least in short-distance interactions, male *A. sagrei* can distinguish between neighbors and nonneighbors, as judged by headbob displays.

Tokarz (1992) found similar results when male *A. sagrei* were confined with potential female mating partners in a male's home cage. Males behaved differently with familiar females than with unfamiliar females. When our results are considered alongside those of Tokarz (1992), they suggest a general ability of male *A. sagrei* to distinguish among familiar and nonfamiliar classes of males and females.

Studies of other lizard species have found patterns of differential behavior that were consistent with the dear enemy phenomenon (e.g., Qualls and Jaeger, 1991; Husak and Fox, 2003). Our results are similar in suggesting reduced aggression toward neighbors. Other studies of *A. sagrei* suggest that fewer bobbing displays are used in contexts where aggression is less likely (McMann, 2000; McMann and Paterson, 2003a; unpubl. data), and we found relatively fewer bobbing displays in interactions between neighbors. Furthermore, in the current study, we found that crest erection that is associated with escalated aggression in male anoles (see Greenberg, 1977; Jenssen, 1979; Scott, 1984) occurred mostly in interactions between nonneighbors.

This study does not necessarily indicate how free-living male *A. sagrei* behave toward neighbors and

strangers. Intact territorial neighborhoods may have emergent properties that were not replicated by our design. For example, differential aggression in intact neighborhoods may be caused by a number of factors. Some, such as fighting ability, may be independent of specific social circumstances. Others, such as a neighbor's interest in competing for a specific parcel of territorial space, can only be elucidated by studies of intact neighborhoods (see Paterson, 2002). Finding an ability to distinguish neighbors from strangers has an important role in determining what kinds of differential aggression are possible in nature (e.g., see Husak and Fox, 2003). However, a growing body of evidence (e.g., Fox and Baird, 1992; Stamps and Krishnan, 1998) indicates that elucidating natural patterns of aggression and their causes will in part require the study of natural territorial neighborhoods.

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Sex Determination and Ontogeny in *Malacochersus tornieri*, the Pancake Tortoise

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ABSTRACT.—We document temperature-dependent sex determination (TSD) in the Pancake Tortoise (*Malacochersus tornieri*). The nesting season is biased toward a fall–winter pattern and the embryos have a postovipositional developmental arrest. Males initially grow faster than females, but females are the larger sex. The species does not readily conform to a hypothesis that TSD is adaptively maintained through a direct association of juvenile growth with adult sexual size dimorphism.

Four testudinids exhibit temperature-dependent sex determination (TSD; Burke et al., 1996), and the Pancake Tortoise (*Malacochersus tornieri*) likely expresses this attribute. There is speculation that TSD adaptively facilitates adult sexual size dimorphism (SSD) by allocating the sex that will become larger to temperatures that yield rapid growth (Webb and Smith, 1984; Rhen and Lang, 1995; Roosenberg and Kelley, 1996). In *M. tornieri*, adult males tend to be smaller in size than females (Gibbons and Lovich, 1990; Moll and Klemens, 1996).

Captive breeding has supplied most information on reproduction in *M. tornieri* (Pauler, 1988; Darlington and Davis, 1990; Schmalz and Stein, 1994), and Moll

and Klemens (1996) summarized observations in the African natural habitat. Here, we report on controlled temperature incubation of eggs, resultant hatchling sex and posthatching growth. We ask whether TSD, if expressed, yields a narrow thermal transition from all males to all females, which can result from natural selection relatively discretely separating males and females (Bull, 1983). Further, are there differences in juvenile growth rates that are apparent from adult SSD? Ewert and Wilson (1996:table 6) noted briefly that early embryos of *M. tornieri* have postovipositional developmental arrest. We examine this phenomenon further with the objective of relating observed development to the natural seasonal environments of the embryos.

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MATERIALS AND METHODS

Given conservation concern for *M. tornieri* (Klemens and Moll, 1995), we relied on captive breeding to

TABLE 1. Incubation times and sex determination according to constant incubation temperatures for *Malacochersus tornieri*. A sex was declared for each tortoise diagnosed. Therefore, $N = 16$ tortoises dissected, $N = 21$ live tortoises grown until secondary sex characters were evident, and an overall total of 37 tortoises were diagnosed without ambiguity.

Incubation temperature (°C)	Development		Development		Sex, postgrowth			Sex, dissection			Sex, both methods		
	N	Laid to Stage 8+ range in days	N	Stage 8+ to pip days \pm SD	N	Males	Females	N	Males	Females	N	Males	Females
27	5	90–101	5	113.4 \pm 6.2	4	4	0	1	1	0	5	5	0
28	13	67–110	13	101.9 \pm 5.8	4	4	0	1	1	0	5	5	0
29	14	50–100	14	94.6 \pm 4.3	0	–	–	9	9	0	9	9	0
30	9	44–98	9	91.9 \pm 4.7	3	2	1	2	0	2	5	2	3
32	19	51–105	19	81.1 \pm 8.3	10	0	10	3	0	3	13	0	13
Total	60		60		21	10	11	16	11	5	37	21	16

provide stock for our research. Eggs came from colonies at the Columbus Zoo (CZ) and nearby. Ambient temperatures were mainly 25–29°C but with warmer patches from heat lamps. Diel cycles were 15:9 h L:D spring–summer and 12:12 L:D fall through winter, and included UV lighting. Long-term breeding groups included one or two males with four to six females. Juvenile tortoises from known incubation temperatures spent their first few years singly or in similar-aged groups of two or three at CZ. Alternate day provision of food for all groups regularly exceeded the amount consumed.

Most females oviposited naturally, but three instances followed oxytocin injection. We used refrigerator type incubators at Indiana University to incubate eggs during the presumed thermosensitive period for sex determination (Mrosovsky and Pieau, 1991). We housed the eggs in boxes of damp vermiculite (0.8 g water:1.0 g vermiculite; \sim –200 kPa). Because direct contact with moist vermiculite risked eggshell rupture that was fatal (in each of four cases), we placed the eggs on small platforms atop the vermiculite. We used a thermometer checked against a NBS traceable standard to monitor incubator temperature. We candled eggs with a fiber-optic lamp to assess fertility and to monitor embryonic development (Ewert, 1985; Beggs et al., 2000). With candling we regarded eggs that showed a subgerminal space within the vitelline sac as fertile (Ewert, 1985). Because there was initial developmental arrest of embryos, we tried several incubation protocols and temperatures (from 20 days at 24°C to continuous 32°C) in attempts to reduce the duration of this arrest (see Ewert, 1985; Ewert and Wilson, 1996). For postarrest development, we adjusted the incubators toward the nominal temperatures of 27°, 28°, 29°, 30°, or 32°C to assess the effects of temperature on sex determination.

We differentially notched marginal scutes of 21 hatchlings according to the temperature at which they had developed as embryos and later inserted PIT tags. During growth, we diagnosed sex from external morphology and from reproductive activity. We dissected nine tortoises that had died unintentionally (during hatching to 10-week posthatching) and seven others from euthanized excess stock (seven- to nine-week posthatching). We assessed reproductive tracts according to Ewert and Nelson (1991).

We determined tortoise “condition” (= live mass/CL) as a measure of fitness for 53 hatchlings. A low ratio indicated a high conversion of yolk to hatchling and, thus, a “good” condition of having achieved more complete embryonic development.

We chose sex as the criterion for evaluating growth because we lacked enough males from any one temperature (27°, 28°, 29°, 30°C) for statistical comparison with females (32°C). We assessed growth in seven males and seven females with the most complete sets of measurements during at least 42 months (some > 5 yr). These tortoises differed appreciably in age in real time, and we did not measure them at given ages. Therefore, we used graphic interpolation to estimate sizes at 30 moths and 42 months. We plotted these estimated sizes against Julian day of hatching, which occurred during eight different months and found no indication of a hatching date effect.

RESULTS AND DISCUSSION

Sex.—Diagnosis of 37 tortoises (Table 1) demonstrated TSD in *M. tornieri* (sex \times temperature interaction: $G = 43.9$, $P < 0.0001$). This total included (1) growth of 21 young tortoises for > 3.4–10 yr ($G = 25.2$, $P = 0.0004$) and (2) dissection of 16 young tortoises ($G = 19.9$, $P = 0.003$). By interpolation (Mrosovsky and Pieau, 1991) the estimated pivotal temperature (yields a 1:1 sex ratio) was 29.8°C.

The TSD pattern of *M. tornieri* conforms to TSD1a of Ewert and Nelson (1991) and thereby conforms to that known for tortoises (Spotila et al., 1994; Eendebach, 1995; Demuth, 2001). Thus, it seems unlikely that *M. tornieri* might yield females from incubation cooler than 27°C. The transition from male-producing temperatures from female-producing temperatures is more discrete than in the tortoise *Gopherus polyphemus* (Demuth, 2001) and some other turtles (Ewert et al., 1994). This discreteness in *M. tornieri* is compatible with selective maintenance of TSD. In some instances, however, a TSD pattern can appear discrete when a nonadaptive, population “bottleneck” truncates a wider variation in the TSD threshold temperatures of the individual embryos (Chevalier et al., 1999).

Reproduction and Development.—Oviposition occurred throughout the year but was biased toward fall-to-winter (93 clutches from August to January vs. 31 from February to July: interval contrast $\chi^2 = 30$, $P <$

TABLE 2. Size and growth of *Malacochersus tornieri* according to sex. All data represent means \pm 1 SD. All comparisons use factorial ANOVA. CL = carapace length.

Life stage	Parameter	Males (N)	Females (N)	F	P
Adults	CL (mm)	146.3 \pm 10.6 (14)	151.6 \pm 9.2 (29)	2.80	0.10
	mass (g)	405.1 \pm 81.7 (14)	470.2 \pm 57.8 (29)	9.07	<0.005
Hatchlings	CL (mm)	40.7 \pm 1.9 (30)	40.0 \pm 2.1 (19)	1.57	0.22
	mass (g)	15.4 \pm 1.6 (30)	14.5 \pm 2.0 (19)	2.76	0.10
Juveniles at 30 months	CL (mm)	124.1 \pm 5.9 (7)	112.5 \pm 5.0 (7)	15.45	0.002
	mass (g)	242.5 \pm 21.6 (7)	233.3 \pm 26.2 (7)	0.52	0.49
Juveniles at 42 months	CL (mm)	140.5 \pm 6.1 (7)	142.2 \pm 7.2 (7)	0.22	0.65
	mass (g)	327.0 \pm 26.8 (7)	332.4 \pm 35.9 (7)	0.10	0.76
Juv. growth: 0–30 months	CL (mm/mo)	2.80 \pm 0.23 (7)	2.42 \pm 0.19 (7)	11.39	0.006
	mass (g/mo)	7.58 \pm 0.75 (7)	7.29 \pm 0.89 (7)	0.43	0.53
Juv. growth: 30–42 months	CL (mm/mo)	1.37 \pm 0.33 (7)	2.47 \pm 0.45 (7)	27.26	0.0002
	mass (g/mo)	7.03 \pm 1.84 (7)	8.26 \pm 1.84 (7)	1.54	0.23

0.0001). This trend was consistent during 11 seasons (Wilcoxon signed-rank test: $z = -2.5$, $P < 0.02$).

The vast majority of clutches (120 of 124) contained a single egg, and the other four clutches each contained two eggs. This mode of one-egg per clutch bears on the several hypotheses to explain TSD (Shine, 1999) because it renders one of them, "sib-avoidance," (Ewert and Nelson, 1991) nonapplicable because it requires more than one sib in the same clutch. For eggs with recorded fates, 58 of 108 eggs (54%) hatched. Apparent fertility of the 108 eggs was 84% but may have been higher because some embryos likely died prior to candling and lost their subgerminal spaces.

The presomite duration of development was always much prolonged and often exceeded the somite/postsomite duration (Table 1). However, we could not place this comparison in exact thermal parallel because we often varied the presomite temperature or used a different temperature for postsomite incubation (see Materials and Methods). None of our presomite protocols shortened the arrest.

Part of the presomite period included extension of preovipositional arrest (diapause I of Booth, 2002). We designated diapause I when the egg contents remained fluid relative to the eggshell during gentle rotation of the egg, which indicates lack of adhesion between the vitelline membrane and the eggshell membrane, as in a freshly laid egg (Ewert, 1985). However, the eggshells of *M. tornieri* never showed an abrupt formation of a chalky white patch, which Booth (2002) used to designate the end of diapause I. Instead, the egg contents became less mobile and broad areas of the eggshell gradually turned white over a week or more.

Diapause I graded into diapause II (attachment of vitelline membrane to shell membrane; Ewert, 1985; Ewert and Wilson, 1996) before development proceeded into its widely recognized serial stages (e.g., Guyot et al., 1994). We did not always closely monitor the transition from diapause I to II because the necessary disturbance of the embryos risked harming them. In 13 instances, a minimum estimate of diapause I averaged 27.9 ± 17.2 days (range 9–61 days), of 82.2 ± 16.9 days (range 47–102 days) for the full duration of arrest. The diapause I and II portions of the full duration were inversely associated ($r = 0.59$, $P < 0.04$), which suggested an indefinite boundary between the two stages in *M. tornieri*. Nonetheless, our designation

of diapause I shared features described for eggs of *Chelodina rugosa* submerged in water (Kennett et al., 1993) and eggs of *C. expansa* that were slow to chalk in air (Booth, 2002). Once *M. tornieri* embryos had advanced to somite stages, the duration of subsequent development varied inversely with temperature (Table 1).

We did not reduce the length of developmental arrest with chilling, which is effective in many turtles (Ewert, 1991). Our protocol for chilling may have been insufficient (i.e., not cool enough, not long enough; Ewert and Wilson, 1996). Alternatively, the type of arrest in embryos of *M. tornieri* may respond to dehydration rather than to chilling, as in another near-equatorial species (*Chelodina rugosa*; Kennett et al., 1993). Unlike *C. rugosa*, however, arrest in *M. tornieri* persists for several weeks after the exterior of the eggshell has become dry and sometimes for days after an internal airspace has formed within the albumen. Thus, we could not clearly

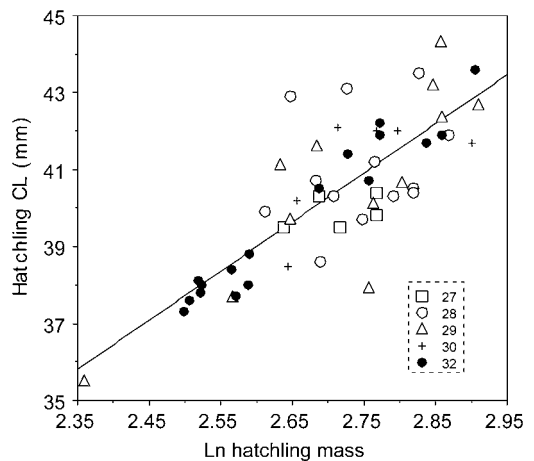


FIG. 1. An index of hatchling condition: the relationship between hatchling carapace length (CL) and mass (g) in the Pancake Tortoise, *Malacochersus tornieri* according to incubation temperature $^{\circ}$ C, symbols in small box). The regression line fitted to all data is: $CL = 12.75 \text{ Ln hatchling mass} + 5.85$.

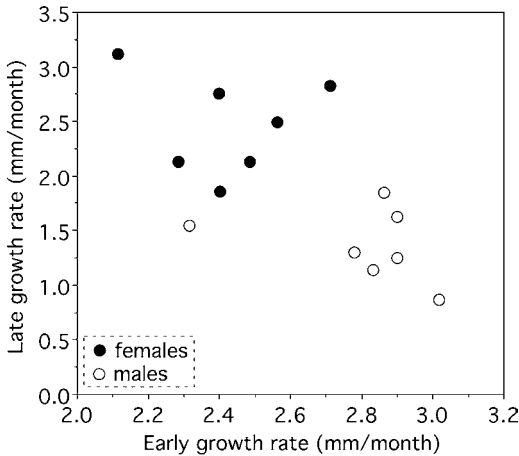


FIG. 2. Early (0–30 months) versus more advanced growth (30–42 months) in carapace length in juvenile Pancake Tortoises, *Malacochersus tornieri* according to sex.

implicate dehydration in terminating arrest of *M. tornieri* embryos.

The distribution of *M. tornieri*, although approximately equatorial in East Africa, extends across a greater area of southern latitudes (Loveridge and Williams, 1957; Klemens and Moll, 1995). Here, the lowest annual solar zenith (“winter”) and the coolest annual weather occurs within the first half of the predominant dry season, which begins in May to early June and extends to October or November (~120–160 days; Wernstedt, 1959; Griffiths, 1972). Anecdotal records of gravid females include April and June (Loveridge and Williams, 1957; Moll and Klemens, 1996). As it seems likely that eggs laid during the wet season would rupture, much as when exposed to damp vermiculite during laboratory incubation, the long period of early developmental arrest may assure that nests are quite dry before the arrested embryos resume development. During this dry period, eggs could develop internal air spaces, which would reduce the risk of eggshell splitting later on. If development resumes by the middle of the dry season, the period of sex determination in embryos would coincide with the thermal “buildup,” which is compatible with the moderately high pivotal temperature for sex determination (Ewert et al., 1994). Our extralimital account of breeding indicates a six-month shift in egg production from the low sun-dry preference for nesting south of the equator to the comparable season north of the equator.

Growth.—Our two criteria for representing size, CL and live mass (Table 2), regularly suggested parallel trends, but adult males and females differed significantly only in mass and growing juvenile males and females only in CL.

After grouping hatchlings by sex (diagnosed or presumed sex according to the temperatures in Table 1; 30 males, 19 females), we used residuals analysis to remove potential egg mass effects and compared condition versus sex. We found no association (ANOVA, $F_{1,47} = 0.007$, $P = 0.93$). Additionally, no association

was apparent for condition versus incubation temperature (Fig. 1). Thus, our conditions for incubation did not appear to have affected initial hatching condition.

At 30 months, males averaged significantly longer than females in CL (Table 2). Among males at 30 months, the declining rank order in CL according to incubation temperature was 28°, 28°, 27°, 27°, 30°, 27°, and 30°C and, hence, did not suggest any simple association with temperature. At 42 months, males and females were not significantly different in size (CL or mass).

Mean growth rates (as CL) of the males exceeded those of females during the first 30 months but then fell behind the females during the next 12 months (Table 2, Fig. 2). Growth rates according to mass suggested a similar trend in early versus late growth for males versus females (Table 2).

Conclusion.—This is the first study of chelonians to monitor the posthatching effects of laboratory incubation temperature from hatching into adulthood (but see Roosenburg and Kelley, 1996). Although males initially grew faster (in CL) than females, females caught up in size as expected from the female-larger adult SSD (Gibbons and Lovich, 1990; Moll and Klemens, 1996; this study). This pattern of early juvenile growth in *M. tornieri* parallels the trend found by St. Clair (1998) concerning Box Turtles (*Terrapene*), that early growth may not reflect adult SSD. As with St. Clair (1998), rapid juvenile growth may be advantageous to males regardless of adult SSD because it hastens their maturity. In the tortoise *G. polyphemus*, however, a conclusive role for growth rate in SSD, seems unlikely because temperatures experienced as embryos did not foster consistent posthatching growth rates across sex and temperature (Demuth, 2001). These observations fail to support a contention that TSD is adaptive because it fosters adult SSD through hastening growth of the larger sex. Thus, caution is needed in interpreting experiments limited to the first few months of posthatching growth. *Malacochersus tornieri* likely is constrained by its crevice-dependent adaptation (Moll and Klemens, 1996). The species, perhaps selected for its small size, likely conforms to Rensch’s rule (relatively small species with female-biased SSD; relatively large species with male-biased SSD; Fairbairn, 1997; example in turtles: Iverson, 1991:fig. 11). Many clades of species including clades with both TSD and non-TSD species conform to Rensch’s rule (Fairbairn, 1997; Kratochvil and Frynta, 2002). Whether juvenile growth and adult SSD are adaptively related to TSD may require a better understanding of Rensch’s rule.

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