

Volume 8, Number 2

April 1998
ISSN 0268-0130

THE HERPETOLOGICAL JOURNAL



Published by the
BRITISH HERPETOLOGICAL SOCIETY

Indexed in
Current Contents

The Herpetological Journal is published quarterly by the British Herpetological Society and is issued free to members. Articles are listed in *Current Awareness in Biological Sciences*, *Current Contents*, *Science Citation Index* and *Zoological Record*.

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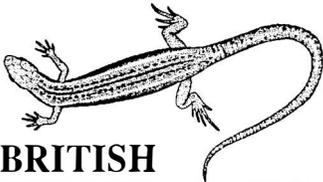
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RESORPTION OF OVIDUCTAL EGGS AND EMBRYOS IN SQUAMATE REPTILES

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Among squamate reptiles, gravid females are frequently said to be able to resorb infertile and malformed eggs from their oviducts. This pattern, if it existed, would allow females to recycle nutrients from abortive attempts at reproduction, and to increase lifetime reproductive potential by modulating reproductive effort according to environmental circumstances. However, a review of the literature reveals that evidence for oviductal egg resorption is weak, and does not preclude other fates for abortive eggs (egg retention or expulsion). Furthermore, for the oviduct to resorb eggs would require that it have the functional properties of the digestive tract, properties that may be incompatible with its several reproductive functions. Future work should not assume oviductal egg resorption in squamates without definitive evidence that the eggs are not simply aborted or retained by females following absorption of water.

INTRODUCTION

In literature dating back to the late 1800s, female lizards and snakes have been said to be able to resorb eggs and embryos from their oviducts under conditions of physiological stress and infertility. Theoretically, such resorption could be an ideal way for a female to minimize loss of nutrients during failed attempts at reproduction, and to control reproduction in such a way as to maximize lifetime reproductive potential. However, as discussed below, evidence for resorption is weak, and several reasons exist to question whether specific squamates actually resorb oviductal eggs, as opposed to aborting them. The purpose of this review is to explore the question of whether squamates can resorb their eggs and embryos, and to encourage individuals with experience in herpetoculture to share evidence bearing on egg resorption in particular species. This issue is of functional, theoretical, and evolutionary significance, and has practical implications for the maintenance and breeding of squamates in captivity.

THEORETICAL ADVANTAGES OF EGG RESORPTION

An ability to resorb eggs and embryos could offer important benefits to female squamates. In typical oviparous squamates, the developing eggs spend about 20-40% of the total developmental period in the oviducts, prior to being laid (Shine, 1983; Blackburn, 1995). Therefore, an opportunity for resorption could exist in egg-layers, as well as in viviparous forms, which retain their eggs to term. By resorbing infertile and malformed eggs, a female could recycle the nutrients that she has invested in her eggs, and thereby enhance her own future survival and reproduction. In oviparous squamates, most or all of the nutrients invested into eggs are in the form of the ovulated yolk, and a similar situation exists in most live-bearing species. In viviparous lizards and snakes, small amounts of organic and inorganic ions are provided to the embryos by the oviduct after ovulation (Panigel, 1956; Hoffman,

1970a; Thompson, 1977, 1982; Stewart, 1989; Stewart *et al.*, 1990). However, as shown by these and other studies (Thompson, 1981; Stewart & Castillo, 1984), the yolk typically provides most of the nutrients for development. Therefore, given that most of female nutrient investment into the prospective neonate occurs at the time of ovulation in both oviparous and viviparous forms, a female that could resorb the yolk or the developing embryo could achieve considerable savings of energy and nutrients.

A second potential advantage of egg resorption is that it would allow females to minimize the physical burden imposed by inviable eggs. Gravity tends to handicap locomotory ability in female squamates (e.g., Vitt & Congdon, 1978; Shine, 1980; Seigel *et al.*, 1987; Cooper *et al.*, 1990; Sinervo *et al.*, 1991; also see Schwarzkopf, 1993). Moreover, in some snake species, females do not feed during pregnancy (Shine, 1980), probably because gravity inhibits passage of food down the posterior gastrointestinal tract. Therefore, by carrying a clutch of inviable eggs, a female would be decreasing her ability to feed, thermoregulate, and escape from predators, with no compensatory advantages.

Thirdly, inviable eggs block the oviducts and would prevent future attempts at reproduction if not removed. The squamate uterus is a thin tube that, in repose, is much smaller in diameter than a single egg. An egg lodged in the uterus could block eggs from subsequent ovulations from being transported through the oviducts, and might well prevent sperm from ascending the tract to the site of fertilization. Resorption of inviable eggs would be an ideal way for females to free up the oviducts for subsequent reproductive attempts.

A fourth potential benefit of egg resorption comes from consideration of life history theory (Stearns, 1992). If a female could resorb eggs under conditions of physiological stress, she could modulate reproduction after ovulation, according to changing environmental circumstances. If conditions were unsuitable (or simply less than ideal) for reproduction, a

female could resorb her reproductive investment and wait until conditions improved to reproduce. Unsuitable conditions could be reflected in unseasonal climatic change, depletion of maternal fat reserves, or food scarcity. A viviparous female that could not resorb or otherwise get rid of her eggs would be "locked in" to pregnancy, carrying the embryos until they were finally born, even at the expense of her own survival. This consideration may be less significant for typical oviparous squamates; given the smaller proportion of the developmental period that eggs reside in the oviducts, the opportunity for females to modulate reproductive investment after ovulation would necessarily be less than in viviparous forms. In the latter, gestation length ranges from several weeks to about a year, depending on the species (Tinkle & Gibbons, 1977; Blackburn & Vitt, 1992); therefore, environmental conditions could change markedly between the period of ovulation and parturition. Consequently, from this standpoint, we would expect the capability of egg and embryo resorption to be particularly advantageous to viviparous species.

DO FEMALE SQUAMATES RESORB OVIDUCTAL EGGS?

An ability to resorb eggs while they are still in the oviducts clearly could have important advantages for female squamates. The question remains, however, as to whether females are able to accomplish such resorption. Uterine resorption of embryos is well known to occur among eutherian mammals, notably certain rodents (Brambell, 1948; MacFarlane *et al.*, 1957; Low, 1978; Gosling, 1986; Westlin *et al.*, 1995). However, evidence for egg resorption among squamates is less clear.

Uterine egg resorption has been inferred for particular species of both lizards and snakes (e.g., Mingazzini, 1892; Domini, 1928; Jacobi, 1936; Clausen, 1940; Kasturirangan, 1951; Parameswaran, 1962; Bustard, 1966; Hoffman, 1970*b*; Yaron, 1972), based on three separate lines of evidence. First, such inferences sometimes are based on observations of oviductal eggs that have stopped developing, or that show no evidence of fertilization. Indeed, abortive or infertile eggs have been reported in the oviducts of numerous squamate species (Giacomini, 1891; Giersberg, 1923; Blanchard, 1925; ten Cate-Hoedemaker, 1933; Jacobi, 1936; Parker, 1940; Neill & Boyles, 1957; Parameswaran, 1962; Badir, 1967, 1968; Hoffman, 1970*b*; Shine, 1977; Powell and Russell, 1991; Gregory *et al.*, 1992; Farrell *et al.*, 1995).

Such observations do not offer *prima facie* evidence of egg resorption, in absence of signs that the oviduct takes up egg components. Non-developing eggs could simply be retained in the oviducts, with or without subsequent expulsion. In the viviparous garter snake, *Thamnophis sirtalis*, for example, Hoffman (1970*b*) found that upon emergence in the spring, the snakes

contained oviductal embryos and adnexae that had been retained from the preceding summer. This also occurs in oviparous species. For example, a female *Diadophis* was reported to retain a fertilized, dead egg for some months (Blanchard, 1925), and a female *Elaphe climacophora* reportedly retained an oviductal egg for more than 16 months (Watanabe *et al.*, 1989). Thus, inviable eggs may be retained in the oviducts, rather than being actively resorbed, even though such retention may have detrimental effects on subsequent reproduction.

Alternatively, malformed or infertile eggs could eventually be expelled by the oviducts and extruded via the cloaca. Squamates are routinely reported to deposit infertile and abnormal eggs, including both oviparous species (e.g., Rollinat, 1904; Neill & Boyles, 1957; Fitch, 1970; Campbell & Quinn, 1975; Dyrkacz, 1977; Murphy *et al.*, 1978) and viviparous species (Jacobi, 1936; Branch, 1973; Branson & Baker, 1974; Mitchell, 1976; Ji, 1995; Ronne, 1996). For example, a captive *Elaphe longissima* female was observed to deposit inviable, deformed eggs of subnormal size; the eggs were not laid as a clutch, but extruded at the rate of one or two a day as the snake crawled around the cage (Lotzke, 1975). In an analysis of 162 *Thamnophis sirtalis* that had been captured and then maintained in captivity, Gregory *et al.* (1992) found that about a quarter of the deposited litters included fully-developed but dead young; another quarter contained one or more undeveloped eggs or young. Interestingly, snout vent length of the live and dead neonates did not differ statistically. Data reported by Ji (1995) on the viviparous *E. rufodorsata* indicate that infertile eggs extruded at the end of gestation do not differ from oviductal eggs collected months earlier, in terms of lipid content or caloric value. One would expect a decline in both parameters if organic components were being resorbed.

As anyone with experience with captive breeding of viviparous squamates knows, extrusion of inviable eggs occurs with great frequency; to breeders they are known as "slugs". In my laboratory, we have frequently observed extruded yolky material in the sandy substrate in my breeding colony of *Chalcides ocellatus*, and recently found small amounts of extruded yolk, surrounded by shell membrane, from captive *Thamnophis* whose oviducts were found shortly thereafter to contain unfertilized eggs. Similarly, we have seen captive *Elaphe gutatta* extrude a small amount of unshelled yolk material prior to oviposition of a normal clutch. Extruded yolk material is easy to overlook, and can dry quickly under a heat lamp or in a sandy substrate. The incidence of infertile eggs, in captive squamates at least, can be high in both oviparous and viviparous species (McEachern, 1991; Ronne, 1996). One must question why infertile eggs are deposited if resorption can occur in the species in question.

A second line of evidence that has been invoked as evidence of egg resorption comes from observations of

oviducts containing eggs that are shrunken and misshapen (e.g., Kasturirangan, 1951). Jacobi (1936, p. 415) published a photograph of the oviducts of the pregnant viviparous slow-worm *Anguis fragilis* in which a single "Abortivei" was considerably smaller than the adjacent normal eggs. Similarly, Domini (1928) illustrated oviducts of the viviparous skink *Chalcides chalcides*, in which eggs were sufficiently misshapen and shrivelled as to suggest loss of egg material. Blanchard (1925) described a female *Diadophis punctatus* with a retained oviductal egg that appeared somewhat shrunken and hardened in the centre. In his comprehensive work on the viviparous garter snake *Thamnophis sirtalis*, Hoffman (1970b) found that half of the pregnant females contained at least one abnormal or developmentally-arrested embryo. The abnormal young were described as being partly mineralized or in a semi-liquified state "apparently indicative of active resorption".

Such observations are suggestive of egg dehydration and necrosis, and perhaps uptake of water by the surrounding uterine tissues. However, observations of dehydrated, abortive uterine eggs do not indicate that the organic components of the eggs and embryos are digested and absorbed by the oviducts, rather than being expelled after water extraction. In fact, in observations of pregnant female *C. chalcides* that contained both normal and degenerating eggs, Domini (1928) found that the decomposing eggs may not disappear from the oviducts until parturition. Likewise, Ronne (1996) described expulsion of dehydrated yolks during parturition of normal young in captive boas.

Definitive evidence of uterine resorption could be provided by histological examination of abortive uterine egg sites. From microscopic study, Mingazzini (1892) inferred that tissues of the oviduct might resorb such eggs in the Mediterranean skink *Chalcides chalcides*, but offered no supportive evidence. Subsequent researchers inferred that captive females of this species resorb their embryos when food is not available (Domini, 1928; Jacobi, 1936), based on observations of oviductal eggs in arrested stages of development. This species is of particular interest from a reproductive standpoint, because it is so highly placentotrophic; females ovulate small (3 mm) eggs and during the three month gestation, provide most of the nutrients for development by placental membranes whose complexity rivals that of therian mammals (Blackburn, 1993a; Blackburn & Callard, 1997). Domini (1928) examined purported uterine resorption sites in two female *C. chalcides*, and described degenerative necrosis of the embryos in some detail. However, his study fell short of offering specific evidence that products of embryo degeneration are taken up by the uterus. In a recent study in my laboratory, we examined a number of abortive egg sites in this species, and found no evidence that egg components are either digested or absorbed by the uterus (Blackburn *et al.*, 1998). The pregnant females

had been obtained through a trans-oceanic shipment, and upon arrival, laparotomy revealed malformed and possibly degenerating oviductal eggs. Our histological examination revealed that the eggs were undergoing dehydration and dissolution, and were in the process of being extruded down the oviducts following absorption of water; in some cases such extrusion was occurring while the embryos were still developing.

Jacobi (1936) examined four abortive egg sites in *Anguis fragilis* histologically. In one of these four sites, he found what he considered to be possible evidence of uterine egg resorption, in the form of a few tiny granules in the connective tissue below the uterine epithelium. While recognizing that the granules were much smaller than yolk droplets of the vitellus, Jacobi (1936) tentatively suggested that they might represent products of yolk digestion. However, the granules were not observed in other "resorbing" females, and Jacobi's (1936) diagram does not rule out the likelihood that they simply represent mast cell granules. Mast cells are common in reproductive tissues of squamates, including the oviduct (Jones *et al.*, 1975; Uribe *et al.*, 1988), and I have observed them in both intact and degranulated condition in abortive egg sites of *Chalcides chalcides*.

In sum, the studies cited above have not demonstrated that female squamates can or do resorb eggs from their oviducts. These studies do not of course preclude the possibility that such absorption occurs, but as discussed below, one can use them to derive criteria for recognition of such resorption.

EVOLUTIONARY CONSIDERATIONS

Given the paucity of evidence that egg and embryo resorption occur among squamates, are we correct in presuming that such a pattern would be advantageous? Probably - after all, selective pressures represent only one factor that affects evolutionary change. Natural selection requires both sufficient time in which to operate and appropriate heritable variation to be present, and the latter may be affected by constraints imposed by disparate functions. For the uterus to undertake egg resorption would require that it be able to accomplish large-scale extracellular digestion of macromolecules, epithelial absorption of the products of such digestion, intracellular breakdown, and finally, export of the products of digestion to the connective tissue where it could be taken up by macrophages or transported away by the circulatory system. Large-scale digestion, secretion and absorption requires enlarged (i.e. columnar) epithelial cells for housing the organelles accomplishing these functions; however, the uterus is adapted in part for physiological exchange with the developing egg, which requires a thinned epithelium. Incompatibility of these functions could constrain a role in digestion, even given sufficient time and strong selective pressures.

As for the temporal parameter, it is useful to keep in mind that egg resorption would probably be most advantageous to viviparous forms. Viviparity in squamates tends to be a relatively recent phenomenon; of the more than 100 origins of viviparity that have been identified among squamates (Blackburn, 1992; Shine, 1985), most have occurred at sub-generic levels, and many appear to be Pliocene or Pleistocene events (Blackburn, 1995). We can only speculate whether this period of time has been sufficient for selection to have conferred upon the uterus the functional attributes of an intestine.

Furthermore, oviductal egg resorption is not the only way for females to recycle nutrients from inviable eggs. Various species of viviparous snakes reportedly eat infertile eggs and dead babies (Ronne, 1996). Captive female *Lepidodactylus lugubris* (Gekkonidae) kept on a poor diet produce deformed eggs with thin shells, which they usually eat upon oviposition (Seufer, 1985). Similarly, female *Phelsuma* kept on a diet deficient in calcium eat their oviposited eggs (Osadnik, 1984). If this pattern is widespread among squamates, recycling of nutrients may offer less of an advantage to oviductal resorption than would otherwise be the case.

Embryo resorption has been widely documented among eutherian mammals (Brambell, 1948; Low, 1978); have these animals not been subjected to the same functional and temporal constraints as squamates? In fact not, because mammalian viviparity dates to the Mesozoic (Lillegraven, 1979; Blackburn, 1993b), and the structure of the eutherian uterus is fundamentally different from that of squamate reptiles. The uterine lining in eutherians forms a thick, glandular endometrium, and the implanting blastocyst penetrates the epithelium in most species, often taking up a position deep in the connective tissue (Luckett, 1977; Mossman, 1987). There, under conditions of resorption, embryonic tissues are susceptible to attack by macrophages and cells of the immune system. In contrast, the squamate uterus during pregnancy is a very thin-walled tube with but a thin layer of connective tissue, and no true implantation occurs. Further, no definitive evidence exists that the uterine epithelium is eroded during pregnancy in any squamate species (Blackburn, 1993c); thus embryonic tissues are not directly exposed to phagocytic cells of the uterine connective tissue.

The paucity of evidence for oviductal resorption of eggs in squamates does not preclude resorption of eggs that have lodged in the peritoneal cavity. Ectopic embryos have been observed in several squamates (Matthews, 1955, 1965), including, for example, members of the snake genera *Vipera* (Bellairs, 1949), *Coluber* (Minton 1949), *Nerodia* (Neill, 1948) and *Thamnophis* (Neill, 1948; Hoffman, 1970b), and the lizard genus *Lacerta* (Dufaure, 1964; Poyntz, 1965). Shine (1977) observed ectopic eggs in females of the Australian snake genera *Pseudechis*, *Notechis*, and

Austrelaps, which he inferred were undergoing resorption. Resorption of ectopic eggs may well occur, since they would be exposed to the motile macrophages, mast cells, and lymphocytes of the peritoneal cavity.

The scarcity of evidence for oviductal resorption of entire uterine eggs also does not preclude uptake by the uterine epithelium of water-soluble organic molecules derived from oviductal eggs. If in fact water is resorbed from abortive eggs, it would be surprising if no such uptake occurred whatsoever. The question remains, however, whether such uptake represents a significant proportion of the yolk lipoproteins, and why egg masses are extruded by female squamates if such uptake is substantial.

FUTURE STUDY

The issue of whether any female squamates can resorb abortive uterine eggs is resolvable with further descriptive and experimental study. Definitive evidence for such resorption could be offered by histological study of abortive egg sites, studies of uterine uptake of labelled molecules incorporated into the eggs, or observations that rule out extrusion of the products of egg decomposition via the cloaca. Conversely, long-term retention of inviable eggs and cloacal extrusion of yolk masses offer evidence against egg resorption. Unfortunately, reports of yolk extrusion and possible egg resorption are less likely to show up in the primary scientific literature than in journals and magazines on reptilian herpetoculture. In fact, individuals with experience in reptile breeding are likely to encounter useful evidence relevant to the issues discussed herein, and could well suggest species as probable candidates for studies of egg resorption. One goal of the present paper is to encourage individuals with such experience to share their information with academic researchers who could benefit from their knowledge.

ACKNOWLEDGMENTS

For offering views on the likelihood of egg resorption, I wish to acknowledge Rick Shine, Craig Schneider, Louis Guillette, Jr., and James Stewart. Craig Schneider and Mary Kuhl called to my attention the abortive eggs in *Elaphe* and *Thamnophis* respectively. Gary C. Packard and one of the anonymous reviewers offered useful comments on the submitted manuscript.

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Accepted: 24.11.97

GROWTH, ALLOMETRY AND SEXUAL DIMORPHISM IN THE FLORIDA BOX TURTLE, *TERRAPENE CAROLINA BAURI*

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Male Florida box turtles, *Terrapene carolina bauri*, grow proportionally longer relative to their height and width, than do females, resulting in a longer, flatter carapace, whereas females develop shorter, higher, and slightly narrower carapaces, possibly as an adaptation to accommodate hard-shelled eggs before oviposition. The subspecies has a typical growth pattern for a North American emydine turtle. Growth is rapid in juveniles, but starts to slow once maturity is reached at an age of 12-13 years. Growth rates approach an asymptote at about age 17 years in males and 16 years in females; very little growth occurs after age 20 years. Florida *T. c. bauri* grows at a slower annual rate than does *T. c. carolina* from Maryland despite having a longer annual activity and growth period. The data presented here may be considered to represent the average growth pattern for *T. c. bauri* in Florida. The cervical scute and all vertebral scutes have a greater width:length ratio in juveniles, but this ratio declines as the scutes lengthen with elongation of the carapace; however, the rate of increase in length varies among the scutes.

INTRODUCTION

Reports of growth and morphometry in eastern box turtles, *Terrapene carolina*, have been confined to the two northern subspecies, *T. c. carolina* (Ditmars, in Pope, 1939; Rosenberger, in Pope, 1939; Ewing, 1939; Nichols, 1939; Allard, 1948; Carr, 1952; Brisbin, 1972; Yahner, 1974; Dodge, Dimond & Wunder, 1978; and Stickel & Bunck, 1989) and *T. c. triunguis* (Leuck & Carpenter, 1981). No growth data have been published for box turtles of peninsular Florida, the most southern portion of the species' range in the United States, and an area where the turtles may be circumannually active (Dodd, Franz, & Smith, 1994). We examined a series of the Florida box turtles (*T. c. bauri*) in the collections of the United States National Museum of Natural History, Smithsonian Institution (USNM) and George Mason University (GMU) to investigate growth, allometry and sexual dimorphism across the geographic range of this subspecies.

Growth rates in turtle populations may vary both spatially (Gibbons, 1967; Christy, Farlow, Bourque & Gibbons, 1974; Ernst & McDonald, 1989; Mushinsky, Wilson & McCoy 1994) and temporally (Ernst, 1971; Tucker, Mahler & Theilung, 1995). The specimens of *T. c. bauri* examined in this study were from several localities over its range, and were collected over an extended period of time. Although any single specimen was probably not representative of its local population, the data are not specific to one population at one time, but instead apply to a large set of times and places within the range. Thus, these data present a picture of the general growth pattern for *T. c. bauri* across its

range. Data from specific localities may not be representative of the growth regime of the entire subspecies. If the localities are from west Florida, particularly along the central and north central coasts, data may show intergradation in the characters of carapace length and shape with the much larger subspecies *T. c. major* whose range lies to the north (Milstead, 1969; Conant, 1975; Ernst, Lovich & Barbour, 1994). A major purpose of this paper is to present a generalized growth profile for the subspecies that can be used for comparison with data from studies performed at specific localities.

Our results are also compared with those of the two northern subspecies, *T. c. carolina* and *T. c. triunguis*, previously reported in the literature. These two subspecies usually stop feeding and become inactive during the colder portions of the year (Ernst *et al.*, 1994), making their growth strategies interesting contrasts with that of the almost continuously active *T. c. bauri* (Dodd *et al.*, 1994).

MATERIALS AND METHODS

One hundred and one *Terrapene c. bauri* (83-166 mm CL) were examined. Each adult turtle was sexed using the characters noted in Ernst, *et al.* (1994); small individuals not showing sexually dimorphic characters were listed as juveniles. All turtles were aged, when possible, by counting growth annuli on the second pleural scute by the method of Sexton (1959) (see also Zug, 1991). The same person counted the annuli on all specimens. Growth annuli are formed in most hard-shelled North American turtles during periods of winter

hibernation, but may also be formed during extended periods of fasting during which the turtle may be active. While *T. c. bauri* does not normally hibernate, temperatures in Florida may drop low enough to cause it to fast for a few weeks in winter, at which time an annulus is formed (Ernst, *pers. obs.*). The accuracy of growth annuli in aging turtles may vary; in Florida *Gopherus polyphemus* (Mushinsky *et al.*, 1994) and in Pennsylvania *Clemmys guttata* and *C. muhlenbergii* annuli have been shown to be accurate estimators of age (Ernst, 1975, 1977). However, Galbraith & Brooks (1987) questioned their use in aging Canadian *Chelydra serpentina*. Subannuli may be formed in more northern populations that undergo variable weather conditions from late spring to early autumn, and these make it more difficult to determine the age of a turtle, particularly if one is not accustomed to such phenomena. Subannuli are shallower and less wide than annuli, and the two can be distinguished with practice (see discussion in Zug, 1991). However, the temperature over the range of *T. c. bauri* in Florida does not become low enough to cause the turtles to stop feeding and form annuli except in winter.

The use of annuli to estimate age is not without potential problems. Within our sample, and mostly among females with at least 20 discernible annuli, some annuli would begin to coalesce at the seams making it difficult to accurately estimate age. Therefore, individuals with annuli that were coalescing but had 20 discernible annuli were categorized in several ways: (1) they were eliminated from the sample; (2) they were put in the 20 year old category; and (3) they were randomly assigned an age between 20 and 35 years. It is believed that *T. carolina* greater than 20 years of age closely approach a growth asymptote and therefore may represent the size at which this asymptote is approached (Stickel & Bunck, 1989). Because more females were characterized by the condition described above, eliminating these individuals from the growth analysis would disproportionately influence the estimation of the female growth asymptote. Analysis of the three data sets described above allows for a discussion of this potentially problematic phenomenon. Maturity was determined by the attainment of the sexually related morphological characters described in Ernst *et al.* (1994).

Measurements recorded from each individual included: maximum parasagittal carapace length (CL), maximum carapace width (CW), carapace height (CH) at the level of the seam separating the second and third vertebral scutes, maximum plastron length (PL), and the widths and lengths of all vertebral scutes (VW1, VL1, VW2, VL2, etc.) and of the cervical scute (CVW, CVL). All measurements were made with dial calipers straight-line to the nearest 0.1 mm.

Growth in turtles has been described by both indeterminate (Stickel & Bunck, 1989; Germano, 1992) and determinate models (Frazer & Ehrhart, 1985; Bjorndal & Bolten, 1988; Lovich, Ernst & McBreen, 1990). Linear models, which assume indeterminate growth, are

best suited to describe growth when relatively brief segments of an organism's total growth are analysed separately. Classification of linear growth analyses into periods of rapid growth and periods of slow to no growth recognizes that growth is not uniform throughout the life of an organism. If the temporal unit is small enough, the predictive value of a linear equation is preserved. However, studies using linear models to describe growth over a large age interval risk misinterpreting growth, especially at the extremities of the fitted line. Where samples are represented by both a wide distribution of body sizes of known ages and by many mature adults, nonlinear models that assume determinant growth may be most appropriate and have the greatest predictive power (Brisbin, 1990).

Because the nature of our data collection methods did not permit longitudinal measurements of growth increments in known individuals, growth was described using an integrated Richards model (Richards, 1959), as modified by Brisbin, White & Bush (1986):

$$L_t = [A^{(1-m)} - (A^{(1-m)} - L_0^{(1-m)}) \exp(-2/T_r(m+1))]^{1/(1-m)} \quad (1)$$

where L_t is the carapace length at time t , L_0 is the estimated carapace length at hatching, A is the asymptotic length, m is the Richards shape parameter, and T is the number of years required to closely approach the asymptote of carapace length. Therefore, in our analysis of growth, L_t represents the carapace length of the preserved specimen at the age estimated by counting the number of visible annuli. For the estimated carapace length at hatchling, (i.e. L_0) the average hatchling carapace length of 32 mm was extrapolated from Iverson (1977).

Unlike fixed-shape mathematical models that are commonly used to describe growth, the shape parameter m of the Richards model can be allowed to vary until convergence, or it can be fixed at a specific value. By fixing the shape parameter at a specific value, the Richards model becomes a fixed-shape sigmoidal model. For example, if m in equation (1) is fixed at 0.667 or 1.0 the Richards model becomes either a Von Bertalanffy or a Gompertz model, respectively (Richards, 1959).

Linear carapace measurements at estimated ages were fitted to equation (1) using a least squares method for nonlinear regression (Proc NLIN; SAS, 1989) with parameters A , m , and T allowed to vary until convergence. Carapace length data were also fitted to equation (1) with the shape parameter m fixed at 0.667 to investigate whether the use of the reduced model resulted in a reduction of the residual error mean square (REMS). Four unsexed juveniles were included in the calculations of both the male and female growth curves.

Allometry of linear measurements was analysed by bivariate linear regression using the method of least squares (Proc Reg; SAS, 1989). Carapace length, plastron length, or carapace width were used as independent variables for regression analyses of other body measurements.

TABLE 1. Shell dimensions (in mm) of male and female turtles examined. Dimensions: CL = carapace length; CW = carapace width; CH = carapace height; PL = plastron length; CVL = cervical length; CVW = cervical width; V1L -V5L = vertebrae 1-5 length; V1W - V5W = vertebrae 1-5 width.

D	Females				Males			
	N	Mean	SD	Range	N	Mean	SD	Range
CL	\	126.78	12.53	83-149	38	137.03	15.11	97-166
CW	45	90.31	10.31	59-110	38	92.71	10.33	71-115
CH	44	66.82	6.95	44-78	36	64.56	6.78	44-76
PL	45	121.18	13.11	81-140	37	126.95	13.47	91-157
CVL	39	7.00	1.97	0-10	38	7.87	2.44	0-12
CVW	39	3.21	1.10	0-5	38	3.16	1.33	0-5
V1L	43	26.63	3.06	20-34	37	27.62	3.66	21-35
V1W	43	25.30	3.79	17-34	37	26.14	3.58	21-39
V2L	39	28.62	3.17	18-33	35	30.23	3.73	22-37
V2W	38	33.18	3.51	26-40	35	33.00	3.77	25-41
V3L	37	27.88	3.62	18.2-33.5	34	29.18	4.25	14.1-35.4
V3W	35	36.26	3.53	26.5-41.2	34	37.86	4.40	26.2-46.4
V4L	38	31.07	4.49	19.1-40.6	35	33.63	5.58	20.0-41.9
V4W	38	32.21	3.72	24.6-40.1	35	33.48	5.06	24.2-46.2
V5L	41	22.73	3.51	14-34	36	24.08	2.98	18-31
V5W	41	30.00	4.28	20-37	37	31.35	3.99	23-41

TABLE 2. Estimated parameters for the Richards nonlinear model where A is the asymptotic length, m is the Richards shape parameter, T is the number of years required to closely approach the asymptote of carapace length; and REMS is the residual error mean square. (One asymptotic standard error in parentheses.) Juveniles turtles were used in both male and female models. N is the number of individuals at least 20 years old which could not be positively aged: ¹eliminated from the sample; ²assigned to 20 years of age; ³randomly assigned an age between 20 and 35 years.

Model/Sex	N	A	T	m	REMS
Richards:					
Female	23 ¹	127.2 (3.5)	15.9 (1.8)	1.472 (1.065)	66.1
	42 ²	134.6 (4.2)	16.6 (3.1)	0.618 (0.818)	75.1
	42 ³	132.5 (2.1)	16.4 (2.8)	0.719 (0.667)	73.5
Male	30 ¹	142.8 (6.1)	17.8 (3.1)	0.989 (1.020)	156.8
	39 ²	142.8 (4.8)	17.8 (3.0)	0.989 (0.957)	146.9
	39 ³	141.5 (3.7)	17.6 (2.7)	1.180 (0.956)	148.3
Von Bertalanffy:					
Female	23 ¹	129.9 (7.9)	15.1 (3.5)	0.667 (fixed)	68.7
	42 ²	134.4 (2.5)	16.7 (1.9)	0.667 (fixed)	73.3
	42 ³	132.6 (2.4)	16.3 (1.8)	0.667 (fixed)	72.7
Male	30 ¹	144.3 (9.6)	17.1 (3.5)	0.667 (fixed)	157.5
	39 ²	144.1 (3.9)	17.0 (2.4)	0.667 (fixed)	143.5
	39 ³	142.7 (2.5)	16.3 (2.5)	0.667 (fixed)	149.9

RESULTS

Male turtles on average were larger than adult females in linear measurements recorded except for carapace height (CH) and the second vertebral width (V2W) (Table 1). A MANOVA revealed significant variation between sexes for CL, CW, CH, and PL (Wilk's Lambda=0.496, $F_{4,75}=19.07$, $P<0.0001$).

Nineteen females and nine males with at least 20 discernible annuli were excluded from the first analysis of growth because their age could not be accurately assessed. The exclusion of the nine males had little effect on the estimation of the growth parameters (Table 2). However, the exclusion of females from the sample had a dramatic affect on the estimation of the upper growth

asymptote and the shape parameter m . This result is not surprising considering that the individuals excluded represent the majority of older animals in the female sample. When the shape parameter was fixed at 0.667 the estimate of the female upper growth asymptote was more similar to the estimate given when all of the data were analysed with the complete model. Given that the estimation of model parameters, such as curve shape m , is often less reliable when a reduced data set is analysed, it may be more appropriate to consider a less parameter-rich model such as the von Bertalanffy model (Lindeman, 1997). Randomizing the age of individuals that were at least 20 years old but could not be positively aged had almost the same effect as classifying these individual as 20 years of age.

TABLE 3. Expected carapace length and percent annual growth based on the growth parameters derived from the complete Richards model.

Age	Female		Male	
	Expected	Percent	Expected	Percent
	CL	Growth	CL	Growth
0	32.00	-	32.00	-
1	44.00	27.27	43.30	26.09
5	85.38	10.33	87.92	11.51
10	114.36	3.57	121.95	3.89
15	126.69	1.31	135.65	1.29
20	131.55	0.49	140.44	0.42
25	133.42	0.18	142.04	0.138
27	133.79	0.12	142.32	0.088

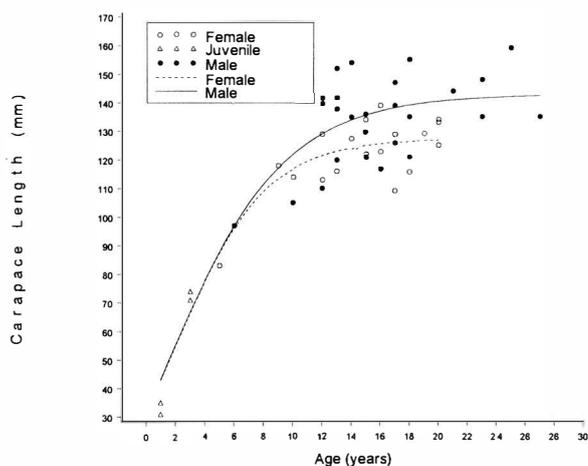


FIG. 1. Richards growth trajectories as a function of age and sex. Four juveniles were included in the calculation of both male and female trajectories.

When all of the data were analysed little difference was observed between the parameters obtained by the complete Richards model and the reduced Richards model (Von Bertalanffy when m is fixed at 0.667). This was especially true for the female growth trajectory where the shape parameter estimated by the complete model was nearly the same as that of the reduced model (i.e. $m=0.667$, Table 2). The male shape parameter more closely resembled that of the Gompertz model (i.e. $m=1$, Table 2).

Growth was fast during the juvenile years, but slowed at 12-13 years in both sexes (Fig. 1, Table 3), approximately at the projected time of maturation, 8-13 years, of *Terrapene c. carolina* (Stickel & Bunck, 1989). By the ages of 17 years in males and 16 years in females growth had plateaued (Table 2). By age 20 growth had nearly ceased in both sexes, averaging < 1 mm per year (Table 3).

Allometric analyses of various carapacial and plastral dimensions showed that males grew proportionally more in length than in either height (Fig. 2, Table 4, ANCOVA $df=1$, $F=49.75$ $P<0.0001$) or width

TABLE 4. Allometric relationships of adult *Terrapene carolina bauri*. Slopes are all significantly ($P<0.001$) different from zero.

x vs. y	Sex	N	Linear relation:	
			$y=a+bx$ (in mm)	R^2
CL vs. CH	F	42	$y=3.67+0.50x$	0.82
	M	34	$y=15.05+0.36x$	0.61
CL vs. CW	F	43	$y=-5.80+0.76x$	0.85
	M	36	$y=13.17+0.58x$	0.72
CL vs. PL	F	43	$y=-7.51+1.01x$	0.94
	M	35	$y=8.61+0.87x$	0.95
PL vs. CH	F	42	$y=8.51+0.48x$	0.84
	M	34	$y=11.89+0.42x$	0.61
PL vs. CW	F	43	$y=3.11+0.72x$	0.84
	M	35	$y=10.38+0.65x$	0.71
CW vs. CH	F	42	$y=15.83+0.57x$	0.71
	M	34	$y=22.96+0.45x$	0.43

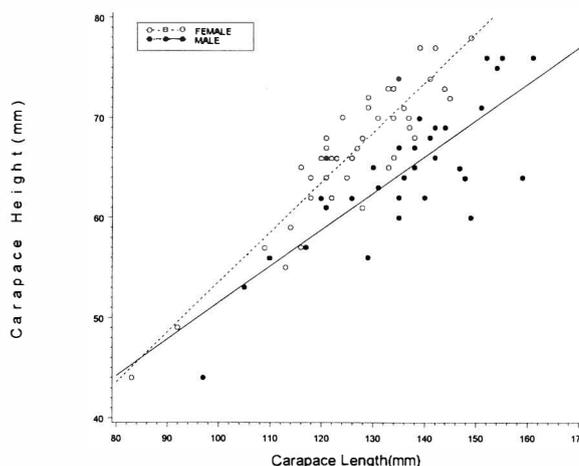


FIG. 2. Allometry of sexually dimorphic carapace height plotted as a function of carapace length and sex. (Female: $CH = 3.67 + 0.499CL$ and Male: $CH = 15.04737 + 0.364CL$; ANCOVA: $df = 1$, $F=49.75$, $P < 0.0001$)

(Fig. 3, Table 4, ANCOVA $df=1$, $F=14.28$ $P<0.0003$). In addition, width increased more than height, producing a longer, flatter carapace than that of females. Allometric growth in females produced a higher, more vaulted, and slightly wider carapace, possibly as an adaptation for shelled-egg storage before oviposition. The plastral hinge was functional in all specimens examined.

The cervical scute and all vertebrae have a greater width: length ratio in juveniles, but this ratio decreases as the scutes grow faster in length than in width while the carapace lengthens (Table 5). However, these scutes increase in length at different rates, resulting in the cervical scute becoming long and narrow, vertebral 1 longer than wide, and vertebrae 2-5 remaining wider than long, although narrowing with age. In adults, vertebrae 2 and 5 are widest, vertebral 4 is the most narrow, and vertebral 3 eventually becomes the shortest in length.

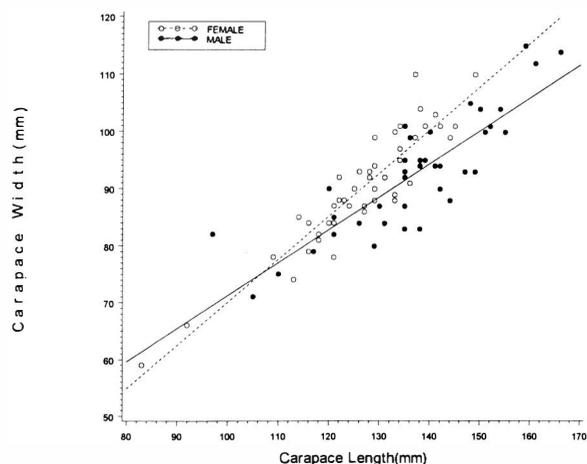


FIG. 3. Allometry of sexually dimorphic carapace width plotted as a function of carapace length and sex. (Female: $CH = -5.796 + 0.758CL$ and Male; $CH = 13.172 + 0.580CL$; ANCOVA: $df = 1$, $F = 14.28$, $P < 0.0003$)

DISCUSSION

The allometric patterns, in which mature male *T. c. bauri* are generally larger in all dimorphic carapace dimensions and grow to produce a longer, flatter carapace than that of the females, are normal for turtles of the genus *Terrapene* (Legler, 1960; Brown, 1971).

Stickel & Bunck (1989) published the only comprehensive report on growth in *Terrapene carolina*, a study of the subspecies *T. c. carolina* on the Maryland coastal plain (which has a shorter carapace length on average than *T. c. bauri*; Conant & Collins, 1991). Their growth/age relationships were determined by bivariate linear analysis, and therefore cannot directly be compared with our results. However, the expected size at a series of ages was calculated with the complete Richards model for both male and female *T. c. bauri* (Table 2) and the values were used to make a general comparison with growth of *T. c. carolina* in Maryland (Stickel & Bunck, 1989). The rapid growth by approximately 27% in the first year by both male and female *T. c. bauri* (assuming an average hatchling carapace length of 32 mm; Iverson, 1977) is similar to the average annual growth rate of 22.8%/yr for juvenile *T. c. carolina* (assuming an average hatchling carapace length of 31 mm in the Washington, D. C. area; Allard, 1948). At 8 years of age male *T. c. bauri* grew 6.03%/yr, and females grew by an average of 5.4%/yr.

However, by 13 years of age the growth rate of Florida *T. c. bauri* declined to approximately 2.0%/yr for both sexes. The large difference in growth rates for even a relatively short time interval emphasizes the potential problems that may be introduced by assuming indeterminate growth. The carapace length of *T. c. carolina* increased at an average rate of 6.8%/yr for males and 5.3%/yr for females between ages 8-13, which is comparable to the growth of *T. c. bauri* at the beginning of the same interval. Between 14-19 years of

TABLE 5. Allometric relationships of carapace scutes (D) to carapace length for adult *Terrapene carolina bauri*. Slopes are all significantly different from zero ($P < 0.05$).

D	Sex	N	Linear relation:	
			$y = a + bx$ (in mm)	R^2
V1L	F	41	$y = 3.83 + 0.18x$	0.53
	M	35	$y = 4.89 + 0.17x$	0.48
V5W	F	39	$y = -1.26 + 0.25x$	0.51
	M	35	$y = 1.54 + 0.22x$	0.66
CVL	F	37	$y = -1.91 + 0.07x$	0.22
	M	36	$y = 5.63 + 0.02x$	0.01
CVW	F	37	$y = 3.39 + 0.00x$	0.00
	M	36	$y = 6.89 - 0.03x$	0.10
V1W	F	41	$y = 1.73 + 0.19x$	0.37
	M	35	$y = 11.41 + 0.11x$	0.21
V2L	F	37	$y = 3.39 + 0.21x$	0.63
	M	33	$y = 1.76 + 0.21x$	0.76
V2W	M	36	$y = 14.22 + 1.16x$	0.29
	F	33	$y = 7.42 + 0.19x$	0.60
V3L	M	35	$y = 1.80 + 0.21x$	0.56
	F	32	$y = -2.39 + 0.23x$	0.70
V3W	M	33	$y = 10.99 + 0.20x$	0.56
	F	32	$y = 5.14 + 0.24x$	0.70
V4L	M	36	$y = -3.57 + 0.28x$	0.62
	F	33	$y = -3.66 + 0.27x$	0.56
V4W	M	36	$y = 8.16 + 0.19x$	0.44
	F	33	$y = -2.55 + 0.26x$	0.63
V5L	M	39	$y = 2.76 + 0.16x$	0.32
	F	34	$y = 4.92 + 0.14x$	0.50

age, male *T. c. carolina* only increased 2.3%/yr in carapace length; female *T. c. carolina*, 3.4%/yr; and both sexes of *T. c. bauri* grew approximately 1.0%/yr (0.5-1.9 mm). After age 19 little measurable growth occurred per year in either subspecies. Ewing (1939) reported an average increase in carapace length of 3.05 mm/yr over a period of 11 years for a female *T. c. carolina* from the vicinity of Washington, D. C. His turtle grew from 93 mm to 126.5 mm, with most of the growth occurring in the first eight years. He estimated the final age of the turtle at 31.6 years.

The pattern of growth shown by both subspecies (rapid juvenile growth, followed by a slowing growth rate once maturity is reached, and a leveling of size increase in later life) is typical for turtles of the genus *Terrapene* (Legler, 1960; Blair, 1976), and North American emydid turtles in general (Cagle, 1946, 1948; Gibbons, 1967; Ernst, 1971, 1975, 1977; Ernst & Ernst, 1973; Lovich *et al.*, 1990; Congdon & van Loben Sels, 1991).

Maturation is an energy-draining process that diverts stored resources, or resources previously available for somatic growth, to gonadal growth and development plus gamete production, formation of secondary sexual structures and sexual behaviours (Bernardo, 1993). In habitats with varying resource availability, the disproportionate allocation of resources to sexual reproduction experienced between males and females may have important implications on the timing of the

development of sexually dimorphic characteristics, such as carapace length. However, because the animals measured in this study were sampled from multiple populations at different times and thus represent an artificial assemblage, it is difficult to make inferences about the factors responsible for the timing of the observed sexual dimorphism, or for that matter any of the other growth parameters estimated. Also, the quantitative comparison of male and female growth trajectories may be limited because juveniles of unknown sex are included in both male and female analyses (Brisbin, 1990). However, the growth pattern may vary only slightly between the sexes during this period (Stickel & Bunk, 1989) and therefore may not greatly influence the estimation of the model parameters.

Studies of *T. c. bauri* analysing the growth of individual populations will be able to address the role of resource limitations on timing of sexual dimorphism as well as other factors responsible for the estimated growth parameters. The study of growth within discrete populations of Florida *T. c. bauri* may also be compared with results presented above, which may represent the average growth pattern experienced by *T. c. bauri*.

ACKNOWLEDGMENTS

We thank W. Ronald Heyer and George R. Zug for allowing us to examine specimens in the USNM, and Ronald I. Crombie and Kenneth A. Tighe for logistical help with the collection. William S. Brown, Terence M. Farrell, Jeffrey E. Lovich, Sheila E. Tuttle and George R. Zug reviewed the manuscript and made suggestions for its improvement.

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Accepted: 17.9.97

BODY TEMPERATURES OF CAPTIVE TORTOISES AT HIGH ALTITUDE IN ZIMBABWE, WITH COMMENTS ON THE USE OF "LIVING MODELS"

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It is difficult to devise physical models which precisely mimic the body temperatures (T_b 's) of large reptiles in the field. Studies of large reptiles have the compensating advantage that individuals can be followed for long periods, so that translocated individuals can be used as 'living models'. We compare T_b 's of two tortoise species in an enclosure in Harare (altitude 1500 m) with those in the field at Sengwa (900 m), where mean air temperatures were about 5°C higher. *Kinixys spekii*, which occurs naturally near Harare, had similar T_b 's at the two sites (means 27.6 and 27.0°C, respectively). *Geochelone pardalis* had significantly lower T_b 's in Harare (29.1°C) than at Sengwa (32.6°C), even though activity was shifted towards midday in Harare. The inability to reach high T_b during activity may explain the absence of *G. pardalis* near Harare, and the distribution of this species in southern Africa.

INTRODUCTION

Physical models of reptiles can be used to estimate body temperatures (T_b 's) in different locations and thus to describe the thermal environment available to an animal (Beaupre, 1995). The use of models to estimate T_b 's is difficult in species of large body size, in which thermal inertia and physiological thermoregulation become important factors. Hollow metal models painted to match the absorptivity of the live animal have been used to measure the operative temperatures (T_e 's) of chelonians (Crawford, Spotila & Standora, 1983; Ellner & Karasov, 1993). The time constants of such models are, however, much lower than those of living animals; models of *Pseudemys scripta* had time constants of 1-2 mins (Crawford *et al.*, 1983), compared to 100-200 mins for living chelonians of comparable size (Hailey & Loveridge, 1997). Even the solid metal models used by Zimmerman *et al.* (1994) showed much faster temperature responses than tortoises. The T_e of a metal model is essentially an instantaneous measure of the potential heat load on an animal, and will only be equal to T_b in equilibrium conditions (Bakken, 1992), which are probably infrequent in active reptiles.

Models incorporating thermal inertia are required to estimate T_b 's of large reptiles, but the physiological thermoregulation of these animals (Bartholomew, 1982) presents another difficulty. The water-filled carapaces of *K. spekii* used by Hailey & Coulson (1996a) only heated at half the rate of living animals, even though they had the same surface characteristics. The difference in heating rates was probably due to physiological thermoregulation, which enables live tortoises to heat faster than they cool (Voigt & Johnson, 1977; Els, Erasmus & Winter, 1988). The bottle models of Hailey & Coulson (1996b) heated at the same rate as tortoises in hot radiant conditions, but are likely to have reached higher equilibrium temperatures due to the

high absorptivity of black paint (Crawford *et al.*, 1983). These models would not give good estimates of T_b 's on cool days, when equilibrium temperatures are important (Hailey & Coulson, 1996a). A particular model can therefore be designed to simulate T_b 's only in some conditions, which complicates comparisons between different environments.

Although it is difficult, perhaps impossible, to estimate T_b 's of large reptiles accurately using passive physical models, large body size has the advantage that individuals can be followed for long periods by radio tracking or thread trailing, and their T_b 's measured by telemetry. This gives the possibility of using translocated animals as 'living models' to assess thermal constraints in different environments, in particular whether T_b can be maintained at the original level by a change in activity period, and if so whether the time available for activity is reduced. As an example, we compare body temperatures of two species of tortoise at an altitude of 1500 m, where only one occurs naturally, with those measured in the wild at a lower altitude.

METHODS

This study used 35 adult *Kinixys spekii* (mean mass 0.7 kg) of both sexes and nine adult female *Geochelone pardalis* (4 kg), each of which was given a unique mark by sawing the edges of the marginal scutes. Tortoises were kept in a large enclosure (100 m²) at the University of Zimbabwe, containing both tall and short grass and some small trees, and provided brassica leaves as additional food. Both *K. spekii* and *G. pardalis* occupy a variety of vegetation types at Sengwa (Hailey & Coulson, 1995), and the habitat in the enclosure was within the range of those occupied in the field (it was structurally similar to bushy grassland, vegetation types h-k of Hailey & Coulson, 1995). Body temperatures were measured with a Yellow Springs Instrument

Co. thermistor with a plastic-covered general purpose probe calibrated against a mercury thermometer. The probe was inserted 2-4 cm into the cloaca (depending on tortoise size) of active tortoises seen between 8.30 and 16.30 hr. Body temperatures were measured on nine days between 8 January and 18 February 1992; all active tortoises which could be located were measured at intervals of 1 hr or more. Body temperatures recorded in Harare (altitude 1500 m) are compared with those measured in the field at Sengwa (900 m) by Hailey & Coulson (1996a). Most (60/63) of the T_b 's of *G. pardalis* from Sengwa were measured in January and February 1992, that is at the same time as observations in Harare. Means are shown ± 1 standard deviation.

Data on the annual variation of air temperature (T_a) at different sites were obtained from meteorological stations at Sengwa and Harare, and from Fullard & Darby (1977), as the mean daily maximum T_a and mean daily minimum T_a in each month. The mean T_a in each month was calculated as the average of these two variables (Meteorological Office, 1996, p viii). Distribution of tortoises is considered in relation to the effective temperature (ET) of different sites, which has been found to be useful in analysing the distribution of snake species in southern Africa (Stuckenberg, 1969).

Effective temperature was calculated as $(8T+14R)/(R+8)$, where T is the mean T_a for the year (averaged across all months) and R is the difference between the mean T_a 's of the warmest and coldest months, all in $^{\circ}\text{C}$ (Stuckenberg, 1969).

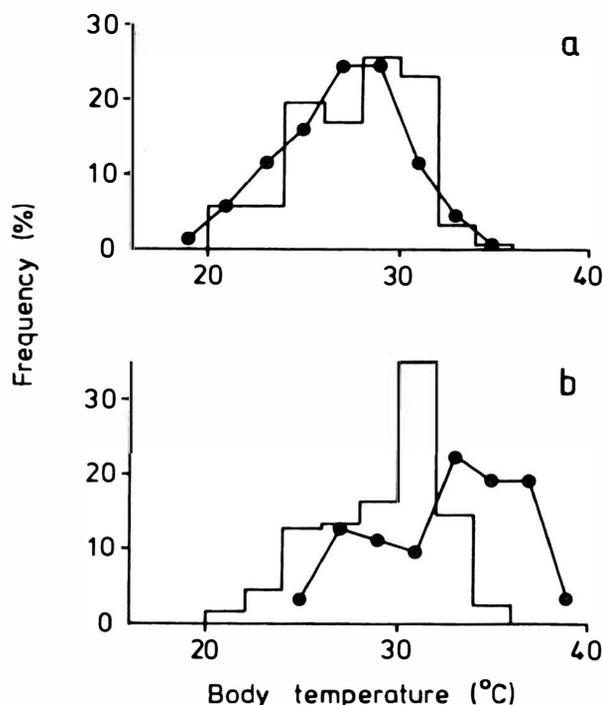


FIG. 1. Body temperatures of *Kinixys spekii* (a) and *Geochelone pardalis* (b) in an outdoor enclosure in Harare (histograms), compared to field measurements at Sengwa (points). Field T_b data are from Hailey & Coulson (1996a).

RESULTS AND DISCUSSION

BODY TEMPERATURE

Frequency distributions of T_b of both species in Harare and at Sengwa are shown in Fig. 1. Body temperatures of active *K. spekii* in Harare had a mean of $27.6 \pm 3.0^{\circ}\text{C}$ ($n=160$), not significantly different from the mean of $27.0 \pm 3.1^{\circ}\text{C}$ found at Sengwa ($F_{1,383}=3.62$, $P=0.058$). Body temperatures of active *G. pardalis* in Harare had a mean of $29.1 \pm 3.1^{\circ}\text{C}$ ($n=174$), significantly higher than T_b 's of *K. spekii* in Harare ($F_{1,332}=19.2$, $P<0.001$), but significantly lower than the mean of $32.6 \pm 3.6^{\circ}\text{C}$ for *G. pardalis* at Sengwa ($F_{1,235}=55.6$, $P<0.001$). There was no significant difference between T_b 's of female, male, and unsexable juvenile *G. pardalis* at Sengwa ($F_{2,60}=0.26$, $P=0.775$). The mean T_b of females at Sengwa ($33.0 \pm 3.8^{\circ}\text{C}$, $n=15$) was slightly higher than that of other animals, so that the low T_b of the *G. pardalis* in Harare was not due to their sex. Analysis of variance showed no significant differences between individual *G. pardalis* in Harare ($F_{8,165}=1.76$, $P=0.088$) or at Sengwa ($F_{42,20}=1.29$, $P=0.271$). Mean T_b 's of the individual tortoises had a mean of 29.0°C in Harare and 32.7°C at Sengwa, very similar to the means of the separate T_b 's given above. The variability of mean T_b between individuals was lower in Harare ($\text{SD}=1.0$, $n=9$) than at Sengwa ($\text{SD}=3.1$, $n=43$) because there were more T_b measurements for each individual in Harare. The mean T_b 's of the individual *G. pardalis* were therefore compared non-parametrically; these differ significantly between

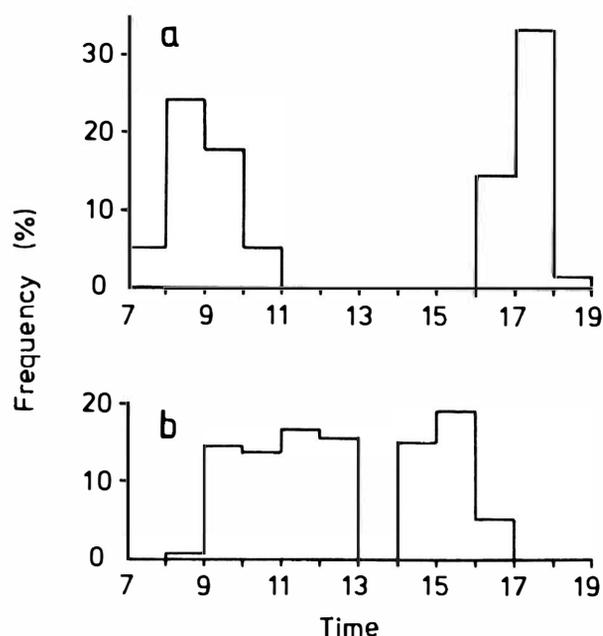


FIG. 2. The times at which body temperatures of *G. pardalis* were measured at Sengwa (a) and in Harare (b). (The gap from 13-14.00 hr in (b) is an artifact of sampling times, not a result of tortoise inactivity.)

Harare and Sengwa (Mann-Whitney test, $P=0.0012$). The identity of individual *K. spekii* was not recorded in Harare, but there were no significant differences between individuals at Sengwa ($F_{31,193}=0.45$, $P=0.995$). Many of these data were from five thread-trailed individuals (Hailey & Coulson, 1996a), which had similar T_b 's: 26.0 ± 2.9 , 26.7 ± 2.9 , 27.0 ± 3.4 , 27.1 ± 3.3 and $27.5\pm 3.7^\circ\text{C}$, respectively.

One major mechanism of thermoregulation in tortoises is to vary the period of daily activity, towards midday in cooler environments (Hailey, Pulford & Stubbs, 1984). Body temperatures of *G. pardalis* in the field were measured in the morning or late afternoon, which was the only time that they were active, while captive animals were measured around midday (Fig. 2). Thus *G. pardalis* had low T_b 's in Harare even though measured at the warmest time of day. There was no evidence that the cooler climate of Harare reduced the time available for activity; the daily activity period was longer there (7-8 hr) than at Sengwa (5-6 hr).

BODY TEMPERATURE AND DISTRIBUTION

Kinixys spekii achieved similar T_b 's in Harare and at Sengwa, despite mean T_a at Harare being about 5°C cooler throughout the year (Fig. 3). This result is not surprising as *K. spekii* has a particularly low T_b for a tortoise (Hailey & Coulson, 1996a), this species occurs naturally around Harare, and its activity at Sengwa was limited on hot days (Hailey & Coulson, 1996a). *Geochelone pardalis* had lower T_b 's in Harare than at Sengwa, despite being active at the hottest time of day. It is possible that the failure to achieve high T_b 's during activity is responsible for the absence of this species around Harare, and in other parts of southern Africa. Fig. 4 shows the similarity between the distribution of *G. pardalis* in this region, and the 16°C isotherm of effective temperature. Fig. 4b shows the cooler area to the east of Harare, from which *G. pardalis* is absent (as shown by the detailed point-location distribution map given by Broadley, 1989).

There are three areas where the distribution of *G. pardalis* does not correspond to the 16°C isotherm of ET. First, along the east coast, where temperatures are raised by the warm southward-flowing Agulhas/Mozambique current (Schulze & McGee, 1978). This discrepancy is common to the tropical herpetofauna assemblage of southern Africa (Poynton & Broadley, 1978). Second, the western region, around Windhoek; and third, south, around Graaff Reinet. Both of these locations have lower ET's than Harare (Fig. 4), but higher mean temperatures during the rainy season when tortoises are active. Mean T_a is higher at Graaff Reinet from December to March (Fig. 3), and at Windhoek from November to March, compared to Harare. (All these sites have peak rainfall during summer, lasting from about November to March, except for Cape Town which has peak rainfall during winter.) It is therefore

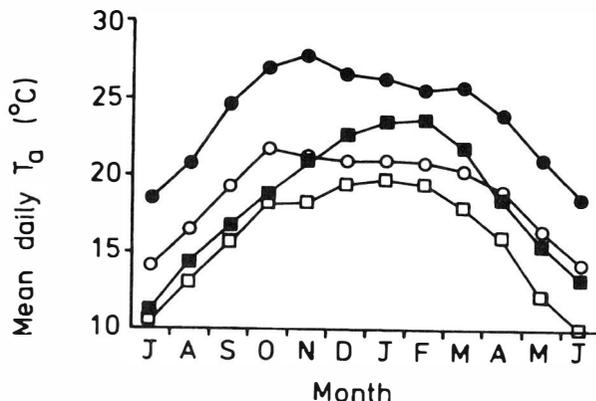


FIG. 3. Annual variation of mean daily air temperature at Sengwa (filled circles), Harare (open circles), Graaff Reinet (filled squares) and Johannesburg (open squares). Data are from Sengwa and Harare meteorological stations, and Fullard & Darby (1977).

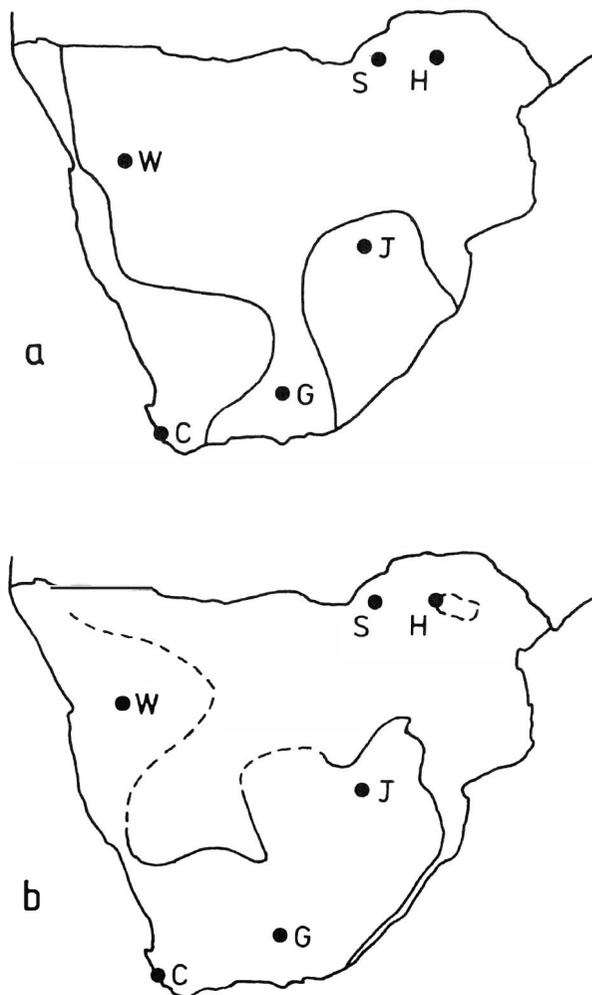


FIG. 4. Maps of southern Africa (south of the Cunene and Zambezi rivers). (a) The distribution of *G. pardalis*, after Branch (1988). (b) The 16°C isotherm of effective temperature, after Stuckenberg (1969). Locations: S=Sengwa (ET= 18.5°C), H=Harare (16.4°C), W=Windhoek (16.0°C), J=Johannesburg (14.9°C), G=Graaff Reinet (15.9°C), C=Cape Town (15.3°C).

possible that the need to achieve high T_b 's during activity restricts the distribution of *G. pardalis* in southern Africa.

Such a restriction assumes that the thermal physiology of *G. pardalis* is evolutionarily inert or static (Bogert, 1949), rather than easily modified or labile (Hertz, Huey & Nevo, 1983); otherwise, populations in cold regions could adapt to low T_b 's. There is no fundamental constraint of moderately low T_b on tortoises, as some species are normally active with T_b 's below 30°C (Hailey & Coulson, 1996a). The 'labile thermophysiology' hypothesis, which is necessary to any analysis of the coadaptation of T_b with performance (Hailey & Davies, 1988) or risk (Hailey & Coulson, 1996a), is gaining support (Diaz, Bauwens & Asensio, 1996). One of the best examples of labile thermophysiology is of a chelonian; Ellner & Karasov (1993) showed that northern box turtles had lower selected and field T_b 's than southern populations. The apparent limitation of activity T_b 's on distribution of *G. pardalis* is thus of interest; it suggests that T_b and thermal physiology are sufficiently resistant to change in this species to prevent its presence in otherwise suitable areas.

Data on the variation of T_b of *G. pardalis* throughout its range are important for the resolution of this question. It is unfortunate that although *G. pardalis* is perhaps the most-studied tortoise in Africa, work on T_b has concentrated on thermal selection in the laboratory (Perrin & Campbell 1981; Zurovsky *et al.*, 1987), rather than field T_b 's.

ALTERNATIVE CONSTRAINTS ON DISTRIBUTION

A constraint on the distribution of *G. pardalis* from habitat or food requirements is unlikely as this species is a generalist in terms of both vegetation types occupied (Hailey & Coulson, 1995) and diet (Milton, 1992; Rall & Fairall, 1993). Alternative thermal factors (other than T_b 's during activity) which should be considered are winter and nest temperatures. Tortoises in the seasonal tropics are inactive during unfavourable periods (Hailey & Coulson, 1996a), and show physiological adaptations to dormancy (Hailey & Loveridge, 1997). It is therefore unlikely that temperatures in winter will limit distribution in southern Africa, as they do not become lethally low (Poynton, 1964). In addition, the 0°C isotherm of July (midwinter) mean daily minimum temperature (Fig. 4b of Schulze & McGee, 1978) encloses an area inland between Cape Town and Johannesburg, cutting across the southern distribution of *G. pardalis*. Both general and specific arguments thus suggest that winter temperatures are not important in limiting the distribution of *G. pardalis*.

Temperatures of nests might also be important (Lambert, 1983), particularly as incubation times of *G. pardalis* are apparently shorter closer to the equator in Zambia (6-7 months; Wilson, 1968) than in Zimbabwe

and South Africa (13-14 months; Bennefield, 1982 and references therein). This explanation also assumes an evolutionarily static variable, in this case the temperature-sensitivity of development. The presence of *G. pardalis* in the south but not around Harare shows that temperatures in summer are more important than the overall annual temperature (as measured by ET). If nest temperature is the limiting factor, this distribution suggests that the long incubation period of over a year includes a pause during winter.

LIVING MODELS

The demonstration that activity T_b 's of *G. pardalis* are limited at high altitude in Zimbabwe thus raises a number of interesting questions about the thermal biology of this species, and shows the potential of translocated animals used as 'living models'. Reciprocal translocations between areas where a species occurs naturally are possible as well as translocations out of the natural range as used here. Animals in the field could be followed by radio tracking or thread trailing, their T_b 's measured directly or by telemetry, and behaviour recorded to show the method of thermoregulation (or its failure) in the new conditions.

Live animals are more difficult to use than physical models, but potentially provide much more information; observations on activity need to be made together with measurements of T_b . Body temperatures of *G. pardalis* in Harare were lower than those at Sengwa, even after the daily activity period had been shifted to midday, showing that tortoises could not compensate completely for the cooler climate. Physical models would show that temperatures were lower in Harare, but not whether changes in activity time could compensate for this. The 3°C difference between T_b 's in Harare and Sengwa was significant; a similar difference between temperatures of models would not be as convincing, given the difficulty of estimating T_b 's from physical models in different conditions.

The statistical analysis of data from such studies requires some attention. The first treatment above used T_b measurements as the unit of statistical analysis. This method assumes that variation between individuals is small compared to the variation between repeated measurements on the same individual. This assumption is valid for physical models measured at long intervals. It was also found to be valid for *G. pardalis*, there being no significant differences between individuals, and results using individual tortoises were similar to those using separate T_b measurements.

Nevertheless, the interchangeability of individuals cannot be assumed in all cases, and should be investigated in each study. Radiotelemetry in particular typically produces large volumes of data from a few individuals; an optimal study would use many individuals for short periods.

ACKNOWLEDGEMENTS

This work was supported by the Research Board of the University of Zimbabwe. We are grateful to Regina Pawaringira for assistance, Evans Chiseya, Luke Madziwa, Lewis Rutsito, and the late Pearson Muhomba for maintaining the tortoises in Harare, Mr Rusirebi and the garden staff for ensuring their food supply, Peter Frost and the late Ian Coulson for meteorological data for Harare and Sengwa, and Michael Lambert and two reviewers for useful comments.

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Accepted: 6.10.97

MORPHOLOGICAL VARIATION IN THE LACERTID *GALLOTIA SIMONYI MACHADOI* AND A COMPARISON WITH THE EXTINCT *GALLOTIA SIMONYI SIMONYI* FROM EL HIERRO (CANARY ISLANDS)

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Morphological variation was investigated in 56 live adult specimens (31 male, 25 female) and ten dead near-hatching embryos of *G. simonyi machadoi* from the "Centro de Reproducción e Investigación del lagarto gigante del Hierro" (Frontera, El Hierro). Dimensions, scalation and teeth traits were measured and quantified. Males and females differed significantly (multivariate analysis of variance) in most of these traits, with values for males being greater than those for females. All traits significantly increased with SVL at a greater rate in males than in females, except for body weight, where no significant difference was found. A qualitative comparison between data from *G. s. machadoi* and those for ten *G. s. simonyi* showed that for most biometric traits, ranges overlapped for the two subspecies, but mean and maximum values were higher in *G. s. simonyi*. Hind limb length increased at a greater rate relative to SVL in *G. s. simonyi* than in *G. s. machadoi*.

INTRODUCTION

The lacertids from the Canary Islands are included within the endemic genus *Gallotia* (Arnold, 1973) and are represented by four living species and one or two that are extinct. Two of the living species are large (up to 265 mm snout-to-vent length): *G. stehlini*, Schenkel 1901 (Gran Canaria) and *G. simonyi* Steindachner, 1889 (El Hierro). The remaining two species: *G. galloti* Oudart, 1839 and *G. atlantica* Peters & Doria, 1882 are smaller (up to 145 mm. SVL).

Two extinct species were giant lizards that have been classified on the basis of biometry and teeth number: *G. goliath* Mertens 1942 and *G. maxima* Bravo 1953. Four extant and extinct subspecies of *G. simonyi* have been described. Now extinct are *G. s. simonyi*, known only from a small islet near the NW coast of El Hierro island, and *G. s. gomerana*, restricted to La Gomera island (Hutterer, 1985). A very reduced population of the subspecies *G. s. machadoi* still persists in the NW of El Hierro island (López-Jurado, 1989). A new subspecies of *G. simonyi* has been recently discovered in the NW of Tenerife (Hernández *et al.*, submitted).

The first data on morphological traits of the living *G. s. machadoi* were published by Machado (1985) and López-Jurado (1989), but due to danger of extinction of this population, few specimens were studied and morphological variation has been reported only in a few cases. The general biology, behaviour and ecology of *G. s. machadoi* is almost unknown. The remaining population lives on a small rocky platform on a very steep inland cliff near Frontera. The species is mostly herbivorous (Machado, 1985), oviparous (4-14 eggs

per clutch) and the reproductive breeding time occurs between May and June-July (Rodríguez-Domínguez & Molina-Borja, in press).

Based on immunological and genetic analyses, some hypotheses have been suggested to explain the origin and later diversification of *Gallotia* forms on different islands of the archipelago (Mayer & Bischoff, 1991; Thorpe *et al.*, 1993a,b). Comparing the results of the latter papers with those of more recent analyses (González *et al.*, 1996), different taxonomic relationships are shown for *Gallotia* species. While *G. galloti* is divided into two lineages (*G. g. galloti* and *G. g. caesaris*) in the study by Thorpe *et al.* (1993a), the traditional subspecies are maintained by González *et al.* (1996). Overall, no clear picture yet exists to explain the present distribution and evolution of the Canarian lizards.

The study of endemic Canarian lizards can thus be considered as important both from an evolutionary point of view and as a means to evaluate different palaeobiogeographic models. With this evolutionary approach in mind, the aims of the present work are: (1) to characterize the morphological variability of living male and female specimens of *G. s. machadoi*; and (2) to compare these parameters with those obtained from published and unpublished data of some specimens of the extinct *G. s. simonyi* and *G. goliath*. The present results present the first quantitative data on living specimens of the endangered *G. s. machadoi*.

MATERIAL AND METHODS

Fifty-six live adult specimens (31 males and 25 females) and ten embryos which died close to hatching of *G. s. machadoi* from the "Centro de Reproducción e

Investigación del lagarto gigante del Hierro" (Frontera) were studied in the present work. Data on some *G. s. simonyi* (Bischoff, unpublished) and fossil *G. goliath* (Castillo *et al.*, 1994) were also compared with those of *G. s. machadoi*.

Twenty-seven biometric traits were measured in all the specimens using the criteria expressed by Pérez-Mellado & Gosá (1988). The traits were (a) Body parameters: body weight (BW), snout-to-vent length (SVL), head length (HL), head width (HW), head depth (HD), fore limb length (FLL), hind limb length (HLL), rostral to anterior eye edge (REE), nostril to anterior eye edge (NEE); (b) Scalation traits: masseteric scale diameter (MSD), number of temporal scales (temporalia, T), supraciliary granules (SG), supraciliary scales (supraciliaria, SS), gular scales (gularia, G), dorsal scales (dorsalia, D), ventral longitudinal scales (ventralia longitudinalis, VL), ventral transversal scales (ventralia transversalis, VT), femoral pores (FP), fourth finger scales (lamellae, L); and (c) dentary traits: number of premaxillary teeth (PT), maxillary teeth (MAX), dentary teeth (DEN) and pterygoid teeth (PTE). A digital caliper (0.01 mm precision) was used to record the biometric data and body weight was obtained by a dynamometer (1 g precision). All individuals of nine years old or less were born in captivity in the "Centro de Reproducción e Investigación del lagarto gigante del Hierro" and maintained (usually in pairs) in outdoor large terraria. The five remaining individuals, aged between 12-16 years old (extrapolated from animals of known age and SVL), were captured in their natural habitat and also maintained in outdoor terraria. The lizards had no predator pressure and were fed *ad libitum* with plant food obtained from the natural vegetation of the area and with insects and newborn mice. The diet was supplemented with vitamins and calcium.

Descriptive statistics were obtained for all traits. Measurements were not independent, so male-female trait comparison was analysed by Multivariate Analysis of Variance (MANOVA, with SVL as covariate). Least square regression analyses (LSR) were also performed to explore the relationship between individual morphological traits and SVL (as the independent variable) within each sex. For LSR, simple linear regression of log-transformed data was used. Slope values for each regression were compared with theoretical values (3.0 for body weight and 1.0 for the other traits) by means of a *t*-test. Analysis of covariance (ANCOVA) was used to compare single body dimensions among sexes taking into account SVL as the covariate (all data log-transformed).

RESULTS

MORPHOLOGICAL TRAIT VARIATIONS IN *G. S. MACHADOI*

Age and weight or size relationships. The relationships between snout-to-vent length and age, and body weight variation and age, of all posthatching lizards are

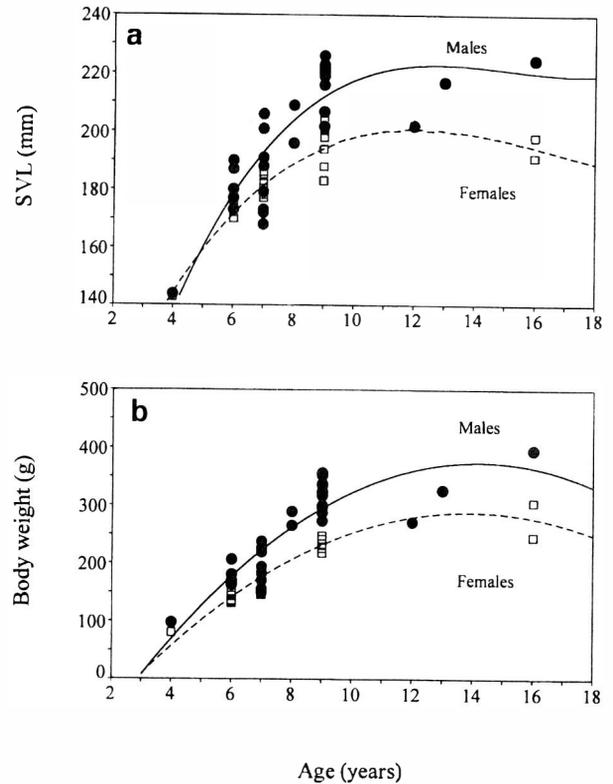


FIG. 1. Growth curves for male (closed circles) and female (open squares) *G. s. machadoi*. SVL (a) and body weight (b) regressed on age.

presented in Fig. 1. The increase in the rate of both traits is greater in the earlier adult stages (4-8 years old), slowing down in the later ones (>8 years old).

Body traits. Mean values, standard errors, range, sample size and coefficient of variation for different body traits of embryos (E), males (M) and females (F) are shown in Table 1a. Males and females differed significantly when considering body dimensions (BW, SVL, HL, HW, HD, FLL, HLL, REE and MSD) with SVL as the covariate (MANOVA, $F_{9,45}=17.08$, $P<0.0001$).

Scalation and teeth traits. Considering scale size and morphology, two zones are distinguished in the temporal region: (1) a central zone around the masseteric scale showing a great variability in number and size of scales; and (2) a tympanic region with small size scales and nearly constant scale number. Some females showed a very reduced scale number in the central zone of temporal region, the scale sizes being of a similar size to the masseteric one.

In the embryos, dentition in dentary and maxillar bones was heterodont. The first five to six dentary teeth are small and incisor-like. The first two had well-developed cuspids pointing to the rear of the mouth. Teeth posterior to the sixth are large, wide and tricuspid with well-developed lateral cuspids. Similar heterodonty is found in maxillar teeth. Adult dentary and maxillar bones also exhibit a similar dentition. Adult pterygoid teeth are usually situated in one row but were aligned in two rows for seven individuals.

TABLE 1. Mean, standard error, range, sample size and coefficient of variation for: (a) Body Weight (BW), Snout-to-Vent Length (SVL), Head Length (HL), Head Width (HW), Fore Limb Length (FLL), Hind Limb Length (HLL), Rostral-to-Eye Edge (REE), Nostril-to-Eye Edge (NEE); (b) Masseteric Scale Diameter (MSD), Number of Temporals (T), Supraciliary Granules (SG), Supraciliary Scales (SS), Gular scales (G), Dorsal Scales (D), Ventral-Longitudinal scales (VL), Ventral-Transversal scales (VT), Femoral pores (F) and fourth finger Lamellae (L) of *G. s. machadoi*, *G. s. simonyi* and *G. goliath*; and (c) teeth numbers: Premaxilar (PRM), Maxillar (MAX), Dentary (DEN) and Pterygoides (PTE) in *G. s. machadoi* and *G. goliath*. * SVL values for *G. goliath* have been extrapolated from the regression function relating Head Length and SVL in *G. s. machadoi* and therefore are approximate figures.

	BW	SVL	HL	HW	HD	FLL	HLL	REE	NEE
<i>G.s.machadoi</i>									
(E)									
mean	-	40.81	12.27	6.07	5.45	17.25	27.0	4.67	3.45
±SE	-	0.85	0.47	0.18	0.16	0.32	0.98	0.16	0.18
range		35.4-43.7	11.4-15.9	5.0-7.0	4.4-6.20	14.5-18.8	20.4-30.4	3.5-5.3	2.5-4.1
n		9	9	10	9	10	10	10	9
CV(%)		6.3	11.6	9.5	9.3	7.0	11.5	11.1	15.6
<i>G.s.machadoi</i>									
(ad. male)									
mean	251.42	198.61	47.98	19.98	26.29	70.82	97.7	21.38	15.99
±SE	13.74	3.85	1.04	0.41	0.72	1.18	1.41	0.43	0.31
range	98-396	144-226	32.1-56.4	15.1-25.1	16.5-34.1	54.4-84.2	79.3-114.2	14.2-24.9	11.0-19.2
n	31	31	31	31	31	31	31	31	31
CV(%)	30.4	10.8	12.1	11.4	15.2	9.3	8.1	11.3	11.1
<i>G.s.machadoi</i>									
(ad. female)									
mean	186.2	182.04	40.08	17.45	22	63.18	88.3	18.23	13.55
±SE	10.44	2.5	0.59	0.29	0.52	0.55	0.75	0.29	0.18
range	81-306	143-204	31.2-45.1	14.6-20.1	15.8-27.0	55.1-67.9	76.7-96.1	14.5-21.4	11.3-15.8
n	25	25	25	25	25	25	25	25	25
CV(%)	28	6.9	7.5	8.5	11.9	4.4	4.3	8	6.7
<i>G.s.simonyi</i>									
(male)									
mean	-	227.6	53.93		31.36	82.16	124.57	-	
±SE	-	4.17	1.87		2.28	1.59	2.91	-	
range		223-236	50.4-56.8		27.4-35.3	79.5-85.0	120-130		
n		3	3		2	3	3		
CV(%)		3.2	6		12.6	3.4	4.1		
<i>G.s.simonyi</i>									
(female)									
mean	-	197.9	45.41		27.48	73.24	92.24	-	
±SE	-	20.65	4.63		4	6.69	6.3	-	
range		119-255	27.4-60.0		14.9-44.2	62.5-99.0	70.0-107.5		
n		6	6		6	5	5		
CV(%)		2.6	2.5		35.7	20.4	15.3		
<i>G. goliath</i>									
1		308.8*	76.84	52.51					
2		361.5*	90.62	-					

Significant differences were also found between male and female scalation: T, F and L (MANOVA, $F_{9,45}=2.72$, $P=0.013$), but no significant difference was obtained when considering teeth (PRM, MAX, DEN, PTE) numbers ($F_{3,52}=1.13$, $P=0.34$).

Isometric/allometric relationships. Male body traits increased with SVL at a greater rate than those for females as shown by ANCOVA (as an example, see Fig. 2 for HL-SVL relationship), except for HD and MSD (Fig. 3) where the contrary occurred. Slopes of regressions were significantly greater than 1.0 for HL and HD in males and for HD and MSD in females (Table 2), and significantly greater than 3.0 in BW for females.

MORPHOLOGICAL TRAIT VARIATIONS IN *G. S. SIMONYI* AND COMPARISON WITH *G. S. MACHADOI*.

Mean values, standard errors, range, sample size and coefficients of variations for the different morphological traits of male (M) and female (F) *G. s. simonyi* are shown in lower cells of Tables 1a, b and c.

A qualitative comparison between *G. s. simonyi* and *G. s. machadoi* reveals that although mean and maximum values are higher (both sexes) in *G. s. simonyi*, there is an overlap in range for most biometric traits.

Overall ranges for the scalation traits are very similar except in the male temporal region where *G. s. simonyi*

TABLE 1b. Details as Table 1a.

	MSD	T	SG	SS	G	D	VL	VT	F	L
<i>G.s.machadoi</i>										
(E)										
mean		56.1	9.66	6.66	29.9	90.6	17.4	37.25	27.88	32.5
±SE		1.42	0.66	0.37	0.58	1.91	0.52	0.75	0.96	0.8
range		50-65	6-13	4-8	27-32	80-99	14-19	35-40	24-33	28-36
n		10	9	9	10	10	10	8	9	10
CV(%)		8.0	20.7	16.8	6.2	6.7	9.5	5.7	10.4	7.8
<i>G.s.machadoi</i>										
(ad. male)										
mean	5.12	63.77	8.94	6.26	31.65	89.55	18.81	35.61	27.74	32.45
±SE	0.14	1.38	0.3	0.19	0.32	0.59	0.25	0.22	0.29	0.25
range	3,7-7,2	50-81	4-12	4-8	27-36	83-95	16-23	32-39	24-32	30-35
n	31	31	31	31	31	31	31	31	31	31
CV(%)	15.8	12.1	18.9	17.0	5.7	3.7	7.6	3.5	6.0	4.3
<i>G.s.machadoi</i>										
(ad. female)										
mean	4.13	56.24	9.44	6.28	31.4	89.0	18.04	35.44	26.24	30.64
±SE	0.13	1.65	0.28	0.17	0.34	0.64	0.21	0.15	0.31	0.39
range	2,7-5,6	39-78	7-13	5-8	27-34	85-96	16-20	34-37	23-29	24-35
n	25	25	25	25	25	25	25	25	25	25
CV(%)	15.8	14.7	15.0	14.2	5.5	3.6	5.9	2.2	5.9	6.5
<i>G.s.simonyi</i>										
(male)										
mean		31.5	14.0	5.0	31.33	94.0	19.0	32.66	30.33	33.0
±SE		1.5	0	0	1.2	3.46	1	0.88	0.33	1
range		30-33	14-14	5-5	29-33	88-100	18-21	31-34	30-31	31-34
n		2	2	3	3	3	3	3	3	3
CV(%)		0.067	0	0	6.6	6.4	9.1	4.7	1.9	5.2
<i>G.s.simonyi</i>										
(female)										
mean		30.6	12.75	5.16	32.33	96.0	20.0	33.86	30.83	33.16
±SE		2.29	0.62	0.16	1.11	1.32	0.72	0.67	1.04	0.4
range		25-39	11-14	5-6	29-36	93-103	18-23	31-36	27-33	32-34
n		5	4	6	6	7	7	7	6	6
CV(%)		16.8	9.9	7.9	8.5	3.7	9.6	5.2	8.3	3
<i>G. goliath</i>										
1	11.72	25	7	6						
2	16.55	21	7	6						

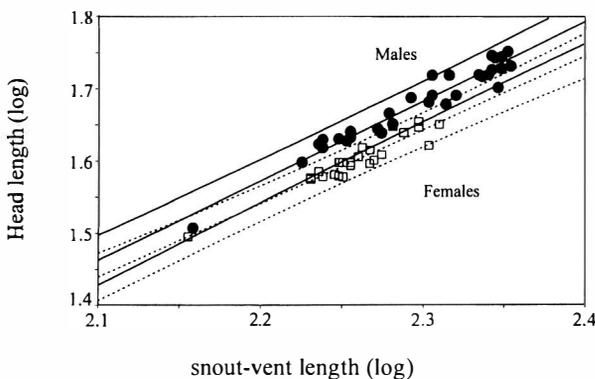


FIG. 2. Relationships of Head Length to Snout-to-Vent Length in *G. s. machadoi* males (closed circles, $HL=0.14 + 1.1 SVL$, $R^2= 94.22\%$, $F=473.06$, $P<0.0001$) and females (open squares, $HL = 0.199 + 1.02 SVL$, $R^2= 89.85\%$, $F=203.53$, $P<0.0001$). Lines lateral to the central regression lines (solid for males and dashed for females) correspond to 95% confidence intervals.

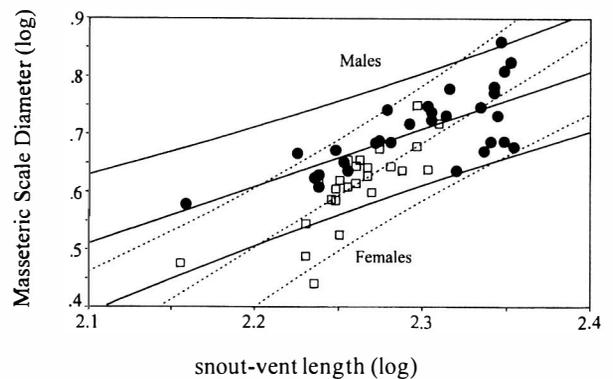


FIG. 3. Regression of Masseteric Scale Diameter on SVL for males (closed circles, $MSD = 0.04 + 0.91 SVL$, $R^2= 52.63$, $F=31.11$, $P<0.0001$) and females (open squares, $MSD = 0.00072 + 1.66 SVL$, $R^2= 67.16$, $F=44.98$, $P<0.0001$). External lines as in the previous figures.

TABLE 1c. Details as Table 1a.

	PRM	MAX	DEN	PTE
<i>G.s. machadoi</i>				
(ad. male)				
mean	6.9	18	21.45	5.12
±SE	0.12	0.2	0.27	0.96
range	6-9	16-20	18-24	3-9
n	31	31	31	31
CV(%)	10.1	6.3	7.1	29.24
<i>G.s. machadoi</i>				
(ad. female)				
mean	6.44	17.4	20.52	4.25
±SE	0.11	0.17	0.29	0.2
range	5-7	16-19	17-23	3-7
n	25	25	25	25
CV(%)	9.1	5	7.2	23.13
<i>G.goliath</i>				
1	9	25	31	18
2	9	25	32	/

has a lower scale number than *G. s. machadoi*. The scale range in the temporal region of females is also lower in *G. s. simonyi* but it is continuous with that of *G. s. machadoi*; this is due to the reduced number of scales in some females of the last subspecies.

Two-way ANCOVA analysis showed that the increasing rate of HLL in relation to SVL was significantly greater in *G. s. simonyi* than in *G. s. machadoi* ($F=75.36$; $df=1,62$; $P<0.001$), significantly greater in males than in females ($F=20.28$; $df=1,62$; $P<0.001$). The effect of interaction between sex and species on HLL was only close to significant ($F=3.92$; $df=1,62$; $P=0.052$), probably due to the small number of data for *G. s. simonyi*.

DISCUSSION

SEXUAL DIMORPHISM IN *G. S. MACHADOI*

Sexual size dimorphism. Mean SVL was significantly higher in male *G. s. machadoi* than in females, as observed in the closely-related species *G. galloti galloti* and *G. g. eisentrauti* (Molina-Borja *et al.*, 1997). Several factors can affect sexual size dimorphism when animals mature at a small size and then continue to grow to a larger asymptotic size (Stamps, 1993), as is the case with *G. s. machadoi* (Rodríguez-Domínguez, unpublished observations). For example, studies have demonstrated sex differences in the size at maturity (Lovich & Gibbons, 1990) and asymptotic size (Dunham, 1978). These factors, in turn, can be affected by several ecological characteristics of the species under study, as for example, differential survival rates of males and females, and sex differences in spatial or temporal distribution (see Stamps *et al.*, 1994 for a review).

TABLE 2. Slopes of the regression lines of different body traits on SVL, and significance levels (P , t -test) of the comparisons with theoretical values (3.0 for body weight and 1.0 for the rest). ** $P<0.01$; * $P<0.05$; NS, not significant).

	Males	Females
Body weight	2.88 NS	3.68*
Head length	1.10*	1.02 NS
Head width	0.89 NS	0.92 NS
Head depth	1.30**	1.49**
Forelimb length	0.78**	0.42**
Hind limb length	0.67**	0.38**
Rostral to anterior eye edge	1.00 NS	0.92 NS
Masseteric scale diameter	0.91 NS	1.66**
Maxillar teeth	0.34**	/
Dentary teeth	0.43**	/

Since all *G. s. machadoi* specimens were raised under the same semi-captive conditions, the resulting sexual size dimorphism cannot be due to ecological factors which differentially affect males and females. It is therefore suggested to be due to intrinsic differential growth rates of males and females (size at maturity is usually lower in females than in males of other *Gallotia* species, Castanët & Báez, 1991). Future research is needed to determine if the same growth patterns occur in free-living *G. s. machadoi*.

Intersexual differences in head parameters. In *G. s. machadoi* relative male head length was significantly greater than female head length (Fig. 2). Previous studies in other Canarian lizards have shown a similar pattern in HL-SVL relationships. For example, in *G. galloti galloti* and *G. g. eisentrauti* (from Tenerife island), males had significantly longer heads than females in relation to SVL (Molina-Borja *et al.*, 1997). Preliminary data show the same pattern for *G. g. palmae* and *G. g. caesaris* (Molina-Borja & Rodríguez-Domínguez, in preparation). However, this pattern of sexual dimorphism was not found in a previous study on *G. stehlini* (Mateo & López-Jurado, 1992). On the other hand, while HL increased at a greater rate in males than in females, the contrary occurred for HD.

Sexual dimorphism in head size could result from sexual selection (Hews, 1990; Anderson & Vitt, 1990) or sexual segregation in resource food utilization (Simon & Middendorf, 1976; Schoener, 1977; Shine, 1990). However, intersexual differences in adult head sizes of herbivorous lizards do not correlate with differences in consumed food sizes (Carothers, 1981; Auffenberg, 1982; Dugan & Wiewandt, 1982). Herbivorous iguanid species having high male aggression usually have a positive HL-SVL allometry (Carothers, 1984). Differential energetic demands in both sexes would presumably have much less effect on head size than on body size, if any. For that reason, head dimorphism might more clearly be a consequence of sexual selection than would body size dimorphism.

Adult *G. s. machadoi* are omnivorous, with a greater proportion of vegetable matter than of insects in

their diet (Machado, 1985), and a possible resource partitioning between the sexes cannot be ascertained at present. On the other hand, although inter-male aggression has been reported (Machado, 1985), there is no specific study of the influence of head size (or any other trait) on male intrasexual competition or mate choice. Therefore, the possible contribution of sexual selection on male head size remains to be determined in *G. s. machadoi* and other Canarian lizards. However, for *G. g. galloti* the contribution of intrasexual competition on male head size has been suggested (Molina-Borja *et al.*, 1998).

Intersexual differences in limb length and pholidotic traits. Our analyses revealed significant sexual size dimorphism in anterior and posterior limb lengths in relation to SVL, those of males increasing at a greater rate than that of females (although the increase rate of limb growth is lower than that of SVL, as reflected in slopes < 1.0). The functional significance of this difference in the increased rate of limb length growth is not known, but it could reflect a need for higher running speed or endurance in males than in females as has been suggested for the adult-juvenile comparison in other species (Huey *et al.*, 1984; Tsuji *et al.*, 1989).

Although males had a larger masseteric scale than females ($P < 0.01$), females did show a greater rate of increase of the masseteric scale diameter in relation to SVL than that of males (Fig. 3).

COMPARISON OF *G. S. MACHADOI* WITH *G. S. SIMONYI*

Overall, *G. s. simonyi* was larger than *G. s. machadoi*. Hind limbs of the first subspecies were much longer than those of the second, both in absolute and relative terms. Relatively longer HLL have been considered and shown to be positively correlated with higher maximum sprint speeds in several lizard species (Garland, 1985; Losos, 1990; Bauwens *et al.*, 1995). This may apply also to the comparison between *G. s. simonyi* and *G. s. machadoi* but data on maximum sprint speed are not available for the second subspecies and cannot be gathered from the now extinct *G. s. simonyi*.

COMPARISON WITH *G. GOLIATH*

A recent study of two mummified specimens assigned to *G. goliath* from Tenerife (Castillo *et al.*, 1994) described for the first time some head external characteristics (see lowest cells of Table 1) and showed their similarities to those of *G. s. simonyi*.

Although statistical comparisons between *G. s. simonyi* and *G. goliath* are not feasible (only two specimens available), the two *G. goliath* individuals measured so far showed much larger SVL and HL values than *G. s. machadoi* and *G. s. simonyi*. Furthermore, *G. goliath* has a higher number of maxillary and dentary teeth than *G. s. machadoi*, a result already reported by previous studies (Mertens, 1942; Hutterer, 1985).

With respect to scalation, *G. goliath* had a lower number of temporal scales than *G. s. machadoi*, but in one case this number is equal to the minimum found in a female *G. s. simonyi*. In contrast, SG and SS numbers are similar in both species.

In conclusion, our analyses revealed that adult males and females *G. s. machadoi* differed in growth curves and also in body traits. The latter increased with SVL at a greater rate in males than in females, except Head Depth and Masseteric Scale Diameter where the contrary occurred. The rate of increase of body weight with SVL did not differ between males and females. Ranges of most biometric traits overlapped between *G. s. machadoi* and *G. s. simonyi*, but mean and maximum values were higher in the second subspecies. For the available data, Hind Limb Length increased at a greater rate than SVL in *G. s. simonyi* than in *G. s. machadoi*.

ACKNOWLEDGEMENTS

To M. Fleitas and E. Gambín, for their assistance in data recording. To Dr. W. Bischoff for allowing us to use his unpublished data on *G. s. simonyi*. To A. Guerra for revising the English. Dr. M. A. González from the Statistics Department helped with data analyses. Part of the present work was supported by a grant given to C. Castillo by Viceconsejería de Medio Ambiente, Canary Government.

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Accepted: 11.3.97

REPRODUCTIVE DYNAMICS OF A POPULATION OF SMALL MARBLED NEWTS (*TRITURUS MARMORATUS PYGMAEUS*) IN SOUTH-WESTERN SPAIN.

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A breeding population of small marbled newts in a temporary pond in SW Spain was sampled over five successive years. Males and females entered the pond just after it flooded in autumn. The adult aquatic season persisted until March or April, with maximum capture rates occurring mostly in January. Several sampling methods were used of which the most efficient was funnel trapping. Recapture rates were low. The population was estimated at about 1000 newts in 1987. Sex ratio did not differ from 1:1 in three seasons. In the other two seasons, which were characterized by low autumn rainfall, males outnumbered females by 2:1, probably as a result of many females failing to enter the pond to breed in those years. In the last two study years, the mean body size of newts was smaller than in previous years, possibly as a consequence of the adverse conditions of the two preceding autumns, which would have had repercussions for the growth of juveniles. An increase in physical condition and individual body mass throughout the aquatic season was observed in both sexes, confirming that the adult aquatic phase is advantageous for growth and maintenance of newts, as well as being necessary for reproduction. The age structure of the population was obtained in one of the seasons. Most males and females were 2-3 years old and a small percentage was one year old. The frequency of 1 year old mature females was lower than that of males. Females showed higher survival rates than males.

INTRODUCTION

Marbled newts show wide variation in body size throughout their range, with populations consisting of small-bodied newts included in a subspecies (*Triturus marmoratus pygmaeus*). This subspecies has recently been extended to include newts from the mid-southern Iberian peninsula (García Paris, Herrero, Martín, Dorda, Esteban & Arano, 1993). Caetano & Castanet (1993) documented variability in growth and longevity in this species and emphasized that more information is needed on geographic variation in the active season of different populations. Díaz-Paniagua, Mateo & Andreu (1996) found that marbled newts from Doñana, Spain, differ from nearby populations in their small body size and earlier age at maturity, which is mainly due to the short juvenile terrestrial phase.

Similarly, geographic variation has been documented for other *Triturus* species, such as *Triturus vulgaris*, which varies in adult size and life history traits across its range (Griffiths, 1984; Verrell & Halliday, 1985a; Accordi, Massarek & Nobili, 1990; Fasola & Canova, 1992). In this species southern populations characteristically have a shorter aquatic period and smaller body sizes (Accordi *et al.*, 1990).

The aim of this study was to document aspects of the reproductive biology of *Triturus marmoratus pygmaeus* in Doñana National Park, showing the intra- and inter-annual variation in sex ratio, abundance, body size and mass of newts during a five year period.

METHODS

Newts were sampled at a temporary pond in Doñana National Park, a sandy area in south-western Spain between the Atlantic Ocean and the marshes at the mouth of the Guadalquivir River (see detailed description in

Díaz-Paniagua, 1990). The pond is usually flooded by autumnal rains and lasts until the summer, which is typically dry and hot in the area. During the newt's aquatic season, the estimated area of the pond ranged from about 60 m² in December 1986 to approximately 880 m² in February 1988, while maximum depth ranged from 16 cm to 120 cm. The vegetation within the pond was mainly composed of meadow herbs on the shores (*Chaetopogon fasciculatus*, *Cynodon dactylon*, *Mentha pulegium*, *Hypericum elodes*, *Juncus heterophyllus* and *Eleocharis multicaulis*) and the hydrophytes (*Callitriche* spp., *Ranunculus peltatus*, *Myriophyllum alterniflorum*) in the deepest areas of the pond. Newts were captured during five successive years (November 1983–April 1988) using different sampling methods. In the first year, newts were captured by dip-netting during the day until no more animals were captured. From November 1984 I also captured newts by hand during the night.

From November 1986, funnel traps were employed following the description in Griffiths (1985) and these were checked three times a night. This method increased the number of newts captured. Each year the pond was sampled once or twice a month from immediately after it formed until no more newts were captured.

All newts captured were measured to the nearest 0.5mm and weighed to the nearest 0.1 g. Body size was estimated from the tip of the snout to the anterior tip of the vent in order to exclude the variation in vent length due to sex and reproductive stage.

Each newt was marked by clipping the longest toe of the right forelimb. The toes were preserved in alcohol for age determination by skeletochronological techniques (see Díaz-Paniagua *et al.*, 1996). The dorsal pattern was photographed and used for individual iden-

tification of toe-clipped newts. Additional information was recorded on the development of the crest in males and on the observation of yolked eggs, clearly visible through the abdominal wall of females.

Because of the low recapture rates, population estimates were only calculated from the sample with the highest capture and recapture rates (February 1987). The number of individuals (N_B) and its standard error (SE) was estimated by the Petersen index, with Bailey's modification:

$$N_B = r(n+1)/m+1$$

$$SE = (r^2(n+1)(n-m)/(m+1)^2(m+2))^{1/2}$$

where r = number of animals caught, marked and released the first day; n = total number of animals captured the second day; and m = number of marked newts captured the second day (Donnelly & Guyer, 1994). The age of newts was estimated for 130 males and 54 females from the sampling period of 1986-87, and for 24 males and 10 females from 1985-86.

Survivorship was calculated from the age structure of the population sampled in 1986-87. Due to the lower frequency of individuals of the one-year class, adult survival was only considered for individuals older than two years, the age at which most individuals mature. Survivorship (l_x) was calculated as the ratio of the number of individuals in age class x to the number of individuals in the youngest age class (Krebs, 1994).

ANOVA was used for comparisons of body length, mass and physical condition of newts. In order to avoid pseudoreplication, all data for recaptured newts were excluded from these comparisons.

RESULTS

THE AQUATIC SEASON

In the study area, the annual aquatic season of marbled newts starts once the pond is flooded, and therefore depends on the autumnal rainfall (Díaz-Paniagua, 1992). In Doñana, the heaviest rains normally fall from October to December, as occurred in 1983, 1984 and 1987. However, in 1985 and 1986 rainfall was low during the autumn, but higher during the next winter and spring (Fig. 1). In 1983 and 1984 the newts first entered the pond in November, while in 1985 they did not enter until December. In 1986 the newts arrived in November, and in 1987 in October. The end of the aquatic season normally occurred in March or early April (Fig. 1), although the pond persisted until June or July. Except for three juveniles, all newts captured in the pond during the study period were adults.

NUMBER OF INDIVIDUALS IN THE POND

The number of different newts captured varied depending on the sampling method and ranged from 65 in 1983-84 to 390 in 1986-87, and the total captures ranged from 70 to 571 (Table 1). However, the rise in

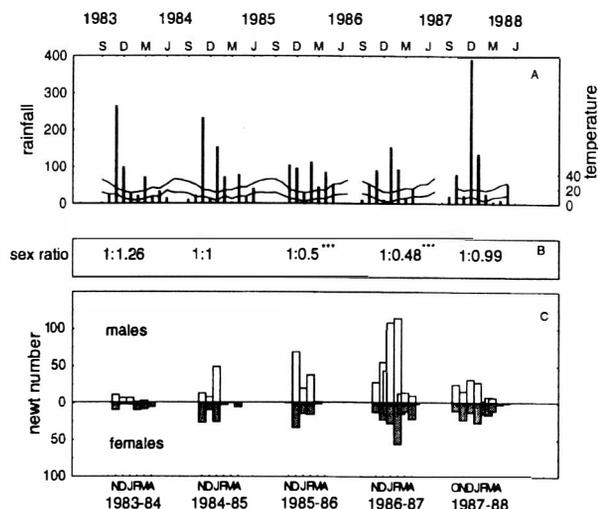


FIG. 1. Variation in (a) monthly rainfall (bars, in mm), and minimum and maximum monthly temperatures (lines, in °C) in the study area; (b) sex-ratio (males:females); and (c) the number of newts captured in the pond in each aquatic season (months are abbreviated by their initials). *** $P < 0.0005$, after χ^2 .

the number of newts observed in 1986-87 was not due to the greater efficiency of the sampling method alone, as twice as many newts were captured than in the following year using the same method. Within each annual aquatic season, the number of newts gradually increased from the onset to a peak in January. By March or April only a small number of individuals was observed (Fig. 1). The maximum length of stay in the pond based on recaptures was 138 days for a male (November 1986 to April 1987), and 112 days for a female (December 1986 to March 1987).

Recaptures from subsequent years were difficult to detect since newts normally regenerated toes and could only be identified by dorsal patterns. Nevertheless, 28 females and 34 males were recaptured in two consecutive years, and five males were caught in three successive years. Nine females and six males were recaptured in alternate breeding seasons.

The estimated number of newts in the pond in February 1987 reached values as high as 530.8 males (SE=194.0) and 443.3 females (SE=128.6)

TABLE 1. Numbers of different male and female newts captured, and the sampling method used in each annual aquatic season (in parentheses, percentage of recaptures).

Season	Males	Females	Sampling method
83-84	29 (6.5)	36 (7.7)	dip-netting
84-85	61 (15.3)	61 (15.3)	dip-netting/ hand capture
85-86	107 (17.1)	44 (33.3)	dip-netting/ hand capture
86-87	259 (32.9)	131 (29.2)	funnel traps
87-88	97 (18.5)	91 (23.5)	funnel traps

SEX RATIO

Males and females entered the pond from the beginning of the aquatic season. Males were twice as numerous as females in the earliest samples of most years, except for November 1984, when females outnumbered males, and November 1983 when the sex ratio was equal (Fig. 1). Males were more numerous than females in the peak sample of all the study years, which (except in 1983-84 and 1985-86) normally occurred in January or February. Females were usually more abundant than males towards the end of the aquatic season (Fig. 1).

The overall sex ratio did not differ from 1:1 in 1984-85, 1985-86 and 1987-88. In contrast, in those years with lower autumnal rainfall, males significantly outnumbered females ($\chi^2_{1985-86} = 20.35, P < 0.0005; \chi^2_{1986-87} = 70.75, P < 0.0005$; Fig. 1). The different sampling methods employed during the study period could have influenced results on sex-ratio, if any of them would have favoured the capture of one sex. However, similar male and female recapture rates in dip-netting sampling (Table 1) suggested similar catchability for both sexes.

The same pattern is suggested by the other sampling methods, since the deviation was not always observed in favour of the same sex.

VARIATION IN POPULATION CHARACTERISTICS

Body size. In males, significant differences were detected between the years. These were mainly due to the smaller body sizes of male newts in the last two seasons (Fig. 2; ANOVA: $F_{4,494} = 88.21, P < 0.0005$). However, significant variation in the distribution of body sizes within each annual aquatic season was only detected in 1984-85 (ANOVA: $F_{3,62} = 2.98, P = 0.038$). In females, significant differences were detected between years for body size (ANOVA: $F_{4,310} = 23.46, P < 0.0005$); the female population also showed lower mean body sizes in 1986-87 and 1987-88. A wide range of body sizes was observed in 1986-87 and 1987-88, while from 1983-84 to 1985-86 mostly large individuals were observed. Significant variation in body size of females during the aquatic season was observed only in 1986-87 (ANOVA: $F_{7,110} = 2.25; P = 0.036$).

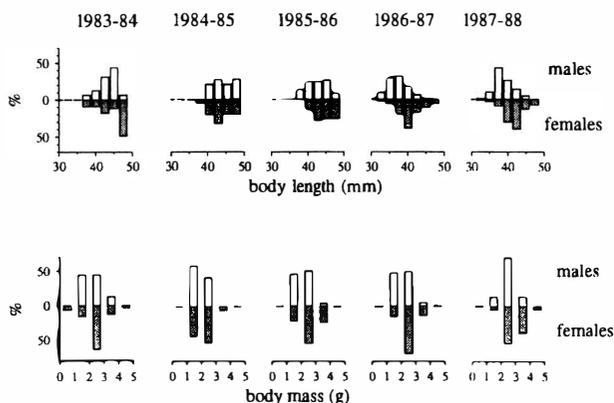


FIG. 2. Distributions of body length and body mass of the newts captured in each aquatic season studied.

Body mass and physical condition. The distribution of male and female body mass in the five study seasons is also given in Fig. 2. Despite the fact that individuals in the pond were smaller in the last two years, they showed heavier body mass than in previous years (ANOVA: males: $F_{4,500} = 4.36, P = 0.0018$; females: $F_{4,323} = 6.52, P < 0.0005$). Body mass (BM) showed a significant correlation with body length (BL) cubed (males: $BM = 0.707 + 0.0003 BL^3, R^2 = 0.543$, females: $BM = 0.706 + 0.0003 BL^3, R^2 = 0.496$) and therefore the ratio $(BM / (BL^3)) \cdot 1000$ was used to analyse the variation in physical condition of newts within the aquatic season. Significant differences were observed between the years (ANOVA, males: $F_{4,492} = 128.21, P < 0.0005$; females: $F_{4,310} = 55.5, P < 0.0005$), but not between males and females (ANOVA: $F_{2,813} = 3.10, P = 0.078$).

There was intraseasonal variation in the last two study years because of the large number of individuals recorded. Females started both seasons with lower index values than males, although both sexes showed a general increase. A decrease in physical condition of males and females was observed in the later samples of both years, coinciding with a decrease in the number of individuals in the pond and with the end of egg laying by many females. In general, males and females finished the aquatic season in a better physical condition than at the onset (Fig. 3).

Recapture data showed an increase in body mass in most individuals throughout the aquatic season. However, weight loss occurred in a few newts that were observed at the end of one season and then recaptured at the start of the next. Data for some males indicated a small or zero weight gain during the first days of the season, yet a large increase later on. Females usually increased weight from the first days onwards (Fig. 4).

Reproductive stage. Females had large eggs in the abdominal cavity from the second sampling period onwards, with a peak of oviposition in January and February, when 100% of females contained large yolked eggs. High percentages of such ovipositing females persisted until March, when only a small number of females were caught.

In 1987-88, males with high dorsal crests were observed from October to February, while low-crested males were detected only at the beginning and at the end of the season. However, during the previous year, 1986-87, when twice as many individuals were caught, males with low crests were observed during the whole

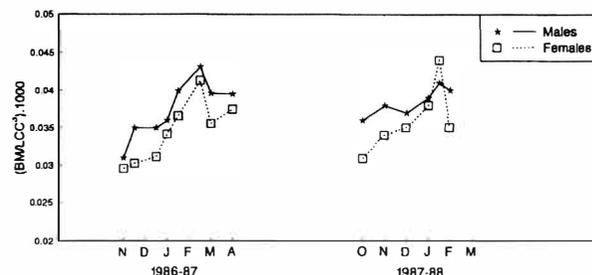


FIG. 3. Variation in the male and female mean physical condition through the last two aquatic seasons studied, 1986-87 and 1987-88.

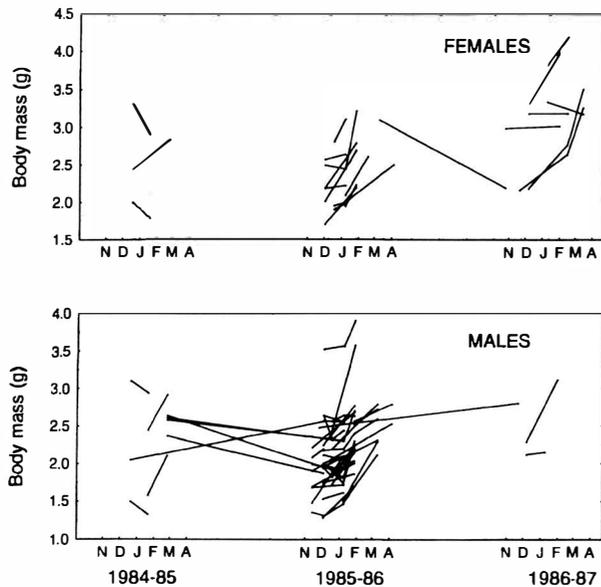


FIG. 4. Variation in body mass of the individuals recaptured during three consecutive aquatic periods.

season, making up about 30% of the males in December and February, and 65% in January.

Age and survivorship. In a previous study we observed that most marbled newts from Doñana matured at two years, with a smaller number maturing at the age of one year (Díaz-Paniagua *et al.*, 1996). In 1986-87, 15% of adult males were one year old, while 60% were 2-3 years old (Fig. 5). Only 5.6% of the female population were one year old individuals, while about 50% were 2-3 years old (Fig. 5). The age of another 24 males and 10 females was estimated for the 1985-86 population, when 12.5% of males were one-year old, and all females were older than two years.

Although 10 year old females were detected in the previous study (Díaz-Paniagua *et al.*, 1996), the maximum longevity detected in 1986-87 was 9 years in both sexes. From the age structure of this season, females showed higher survival rates than males, since there were higher proportions of females than males more than two years old (Fig. 5).

DISCUSSION

Pond flooding marks the end of Doñana's marbled newts annual inactive period during the hot and dry summer months. The unpredictability of flooding confers a characteristic inter-annual variation to the onset of the newt aquatic season. In contrast, there is no flexibility at the end of the season. Although the pond normally lasted up to June or July, the last newts were commonly found in March, or rarely, in April when the first larvae hatch (Díaz-Paniagua, 1992).

As in other newt species (Verrell & Halliday, 1985*a,b*), the aquatic season should not be considered as just a reproductive season, but also as being important for the maintenance and growth of individuals. Although mating and oviposition are important activities, they do not cover the entire aquatic period, in which a substantial increase in body length (Díaz-Paniagua *et al.*, 1996) and mass occurs for both sexes.

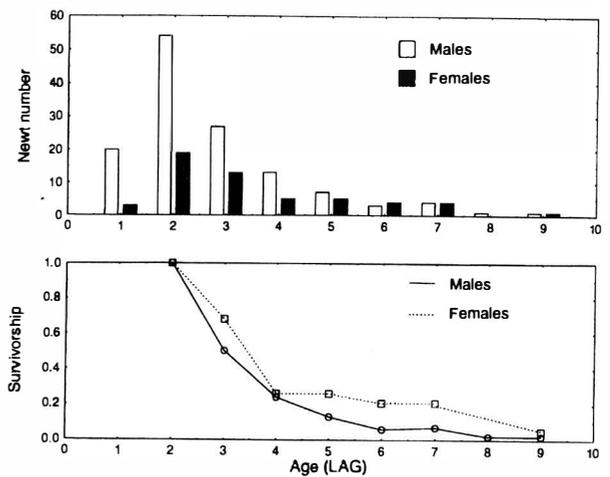


FIG. 5. Age structure and survival rate of male and female populations in 1986-87. LAG = lines of arrested growth in phalange sections of newts.

In other studies of newt populations, substantial weight loss occurred throughout the aquatic season (Harrison, Gittins & Slater, 1983; Andreone & Giacoma, 1989). The benefit obtained during this season probably depends on the productivity and duration of the breeding habitats, which may sometimes be adverse and uncertain. The newt population in Doñana is at the southern limit of the range of the species, where small size and early age at maturity may be adaptations to a highly unpredictable environment (Begon & Mortimer, 1986). The dry and hot summer conditions in this area are likely to constrain the annual activity period of newts to the aquatic season, when, together with their reproductive effort, other activities must be important for survival and growth of individuals. Northern populations of *T. m. marmoratus* are probably constrained by lower winter temperatures, as they breed later in the year in northern Spain, from February to May (Braña, 1980; Salvador, Alvarez & Garcia, 1986). At the northern limits of the species range, marbled newts stay in ponds from March to June (Bouton, 1986). Southern Portuguese newts have an aquatic season similar to that of newts from Doñana (Caetano & Castanet, 1993). However, compared to the Doñana population, the Portuguese newts attain maturity at a later age and are characterized by larger body size and greater longevity (see Díaz-Paniagua *et al.*, 1996).

Males and females seem to have different dynamics, considering the wide within-year and between-year differences observed in sex ratio, and their different survival rates and age structures. Both sexes entered the pond at similar times, and individuals may persist there for a long time. Residency in the pond is longer than that detected for a population of *T. m. marmoratus* in northern Spain where maximum residence of adult newts in a pond was 56 days (Salvador *et al.*, 1986). Fasola & Canova (1992) found wide variation in the annual period of residence in water among three species of *Triturus* coexisting in the same pond. The

species with shorter residence used the pond exclusively for reproduction, while the other species persisted in the pond after reproduction, when newts could perform other activities which would favour growth. Verrell & Halliday (1985a), studying a population of *T. vulgaris*, reported that body mass declined over most of the aquatic season, and only increased in those newts that remained in the pond after breeding. In Doñana, most newts gained weight as soon as they entered the water, and the gradual increase in overall physical condition revealed that the aquatic season was advantageous for both sexes. The highest male reproductive effort takes place early in the season, after they have developed their crests, while during the late season they are probably mainly devoted to feeding and growth. Females, however, make an important investment in reproduction over a longer period. From an early stage in the active season they initiate the process of egg yolking and make a great investment later in the season during egg-laying, with the peak of oviposition being in February. Up to this time females showed a notable weight gain, and became extremely voracious. Although egg deposition must represent a great effort and a considerable weight loss, they finished the aquatic season in better condition than at the onset of the season.

A wide range of variation in sex ratios has been observed for other *Triturus* populations during the aquatic season, with an excess of males (Hagström, 1979; Harrison *et al.*, 1983; Griffiths, 1984; Andreone & Giacoma, 1989), equality (Verrell & Halliday, 1985b), and an excess of females (Bell, 1977; Verrell & Halliday, 1985a; Salvador *et al.*, 1986). The skewed sex ratio was explained in *T. vulgaris* populations by a differential mortality of individuals of one sex because of their greater reproductive effort (Bell, 1979; Harrison *et al.*, 1983), which was supported in one of these populations by the observation that females lost weight during the breeding season. In the present study, equality was observed in most of the years, but in those seasons of lower autumnal rainfall, males were twice as abundant as females. The age structure in one of these years (1986-87) revealed a higher proportion of young males than of females, while in the smaller sample of 1987-88, when the sex ratio was also skewed, all females were older than two years, and 12.5% of males were one year old. This certainly contributed to the unequal sex ratio.

The early months of the season, when females are replenishing their physical condition and yolking the eggs, must be a requirement for one year old females to initiate breeding, which is thus improbable in seasons with delayed rainfall. The scarcity of resources in autumn may also have negative effects on those older females which could not reach adequate physical condition for oocyte maturation and ovulation. This, in turn, could explain why some females did not reproduce in such years. The lower reproductive frequency of females would also explain the result of the differences in age structure of the sexes, with higher survival

rates among females. The recapture data confirm that females may reproduce in two successive years while males were confirmed for three successive breeding seasons. Accordi *et al.* (1990) also found variation between years in sex ratio in a southern population of *Triturus vulgaris*, because not all females entered the pond in dry years. Griffiths (1984) commented on the possibility of non-annual breeding of a proportion of females in an English population of *T. vulgaris*. In Doñana, during a drought which lasted from 1991 to 1994, I observed an attempt at breeding in January 1994, when the pond studied was ephemerally flooded. The population sample consisted of 23 males and only five females (male:female ratio, 1:0.27), confirming the lower availability of breeding females under suboptimal conditions.

Verrell & Halliday (1985a) also found a variation in the operational sex ratio over the breeding season, due to the synchronicity of female ovulation, while males were able to maintain courtship activity and produce spermatophores over a prolonged mating season. A similar variation was observed by Griffiths (1984), who found a slightly male-biased sex ratio in the aquatic population, while females outnumbered males outside the pond. In the present study variation was also observed within most of the seasons. During the first part of the season there were more males than females, while in the second part, females were more numerous, probably because they are obliged to persist in the pond to conclude oviposition.

Despite the low autumn rainfall and the 1985-86 and 1986-87 skewed sex ratio already discussed, the number of captures was high during these periods. However, although abundance cannot be compared in both years because of the different sampling methods employed, high population size was estimated in both periods. In 1987 the population size was estimated to be approximately 1000 individuals and the pond extended over some 540 m². This can be regarded as a high density of newts, if compared with other dense newt populations (Glandt, 1982; Verrell & Halliday, 1985a; Miaud, 1991). The decrease in abundance detected in 1987-88 could be explained by lower reproductive success of the population in 1985-86, when the skewed sex ratio suggested that an important fraction of the female population did not breed.

The last two seasons studied differed from the previous years in (1) mean body size of newts, which was smaller than in previous years; and (2) a general increase in body mass. The smaller body size could be explained by higher recruitment of young adults from the preceding years; however, the similar proportion of one-year males in 1986-87 and 1985-86 does not support such an idea. Rather, the smaller body size could be a consequence of the seasons of scarce autumn rainfall, with a shorter activity period which could have repercussions on the growth of individuals, in particular those newts which did not breed and juveniles which would mature at the age of one or two years at a smaller body size. An *a posteriori* Duncan Test showed that the

overall heavier body mass was significantly different in 1987-88, after a very rainy year, when the size of the pond increased in size and probably in resource availability.

ACKNOWLEDGEMENTS

This study was financially supported by DGICYT (project PB-91-0115-C02-02) and Junta de Andalucía (Grupo RNM 0128). Rosario Rivas encouraged me and assisted in the fieldwork. I thank Claudia Keller and Ana Andreu for their critical reading of the manuscript; and T. R. Halliday, J. W. Petranka, M. Sparreboom and B. Arano, for their comments.

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Accepted: 5.6.97

REPRODUCTION OF THE VIVIPAROUS LIZARD *LIOLAEMUS ELONGATUS* IN THE HIGHLANDS OF SOUTHERN SOUTH AMERICA: PLASTIC CYCLES IN RESPONSE TO CLIMATE?

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Squamate viviparity has evolved on several occasions, and probably independently within the genus *Liolaemus* itself. Hypotheses about the origin of reptilian viviparity emphasize the advantage of providing an adequate thermal environment for the embryo. At the same time, high latitudes and altitudes limit the availability of heat to perform vitellogenesis and gestation. The genus *Liolaemus* includes both oviparous and viviparous modes of reproduction, as well as reproductive cycles with great variations in the timing of the events. In the present work maximum juvenile size, sexual dimorphism, gonadal cycle and litter size of viviparous *Liolaemus elongatus* were studied. Female lizards may have annual or biennial cycles, but males reproduce annually in synchronization with the female cycle. Phenotypic plasticity may be one way that allows the species to cope with environmental constraints, and may be a reproductive adaptation that *Liolaemus* has evolved in response to the cold climate in the highlands of southern South America.

INTRODUCTION

Viviparity has arisen in the squamate reptiles on multiple occasions (Packard, Tracy & Roth, 1977; Blackburn, 1982; Guillelte, 1993), and probably independently within the genus *Liolaemus* itself (Blackburn, 1985; Espinoza, 1996). The relationship between reptilian reproduction and the environment may be the consequence of ecological factors (Vitt, 1992) as well as inherited traits that evolved in the past (Guillelte & Méndez la Cruz, 1993; Heulin, Osenege & Lebouvier, 1991). The family Liolaeminae has been subject to the consequences of tertiary orogeny and glacial fluctuations (Cei, 1993) and probably many of its phenotypic characteristics are related to these events.

The cold climate hypothesis (Packard *et al.*, 1977; Shine 1983; Shine, 1985) considers viviparity to have evolved as an adaptation to low temperature conditions, among other factors. The strong relationship between embryonic developmental rate and temperature (Shine 1983; Heulin *et al.*, 1991; Van Damme, Bauwens, Braña & Verheyen, 1992; Shine & Harlow, 1993) establishes the main constraint to reproduction in relation to the shortening of activity season in high latitudes. Espinoza (1996) proposes this hypothesis to explain the origin of viviparity in the genus *Liolaemus*.

Van Damme *et al.* (1992), Shine & Harlow (1993), and Shine (1995) tested the idea that a given range of temperatures during embryogenesis directly enhances hatchling viability. The phenotypic plasticity hypothesis (Shine, 1995) predicts that prolonged uterine retention might enhance offspring fitness in any environment in which maternal temperatures differ from nest temperatures. Evidence in support of this hypothesis is far from comprehensive (Heulin *et al.*, 1991; Sinervo & Adolph, 1994; Martín Vallejo, García

Fernández, Pérez Mellado & Vicente Villardón, 1995; Shine, 1995). A complementary approach is that of Charland (1995); (see also Charland & Gregory, 1990; Packard *et al.*, 1977), i.e. the advantage of viviparity lies in the acquisition of a narrow range of developmental temperatures.

We can expect that pregnant females thermoregulate to offer a stable thermal environment to developing embryos while vitellogenic females require an optimum body temperature to minimize vitellogenesis lapse. Both processes require adequate access to heat. Although thermoregulation in lizards is extensively described, how females respond during gametogenesis and pregnancy is little-known (Charland & Gregory, 1990; Charland, 1995; Ibarzüengoytía & Cussac, 1996).

There are four responses that may result in multiannual cycles: (1) prolonged vitellogenesis (van Wyk, 1991; Cree & Guillelte, 1995; Cree *et al.*, 1992); (2) prolonged pregnancy (Vial & Stewart, 1985; Cree & Guillelte, 1995); (3) allocation of vitellogenesis and pregnancy in separate breeding seasons (Ibarzüengoytía & Cussac, 1996); and (4) skipping of a year (van Wyk, 1991). Annual cycles can be tested by three criteria: (1) a high ratio of non reproductive females during the breeding season (Aldridge, 1979; van Wyk, 1991); (2) the simultaneous presence of individuals with reproductive conditions non adjacent in the cycle sequence (Cree & Guillelte, 1995), and its corollary, (3) the simultaneous presence of vitellogenic and pregnant females in the population (Ibarzüengoytía & Cussac, 1996).

The genus *Liolaemus* is distributed from the highlands of Perú and Bolivia to Tierra del Fuego and from Pacific islands to Brazil (Cei, 1986). *Liolaemus* include oviparous and viviparous modes. Viviparous species

show great variations in the timing of reproductive events. *Liolaemus multififormis multififormis* (4600 m), *L. alticolor*, *L. jamesi*, *L. aymararum* and *L. huacahuasicus* (3700 m) exhibit autumn vitellogenesis and ovulation, followed by pregnancy over winter and parturition during spring (Pearson, 1954; Leyton *et al.*, 1982; Ramírez Pinilla, 1991). Three mountain species (2500 m), *L. altissimus*, *L. leopardinus*, and *L. nigroviridis* (Leyton & Valencia, 1992), exhibit vitellogenesis from late summer to early spring, followed by pregnancy during spring and summer, and the same situation occurs in *L. gravenhorsti*, a mid-elevation (700 m) lizard (Leyton & Valencia, 1992). *Liolaemus pictus* responds to short and cold activity seasons by means of biennial or triennial cycles, allocating vitellogenesis and pregnancy in different years, and sometimes combining the lengthening of the ovarian cycle with the skipping of a year (Ibargüengoytía & Cussac, 1996).

Liolaemus elongatus has been always described as a saxicolous species dwelling in the steppe (Ceï, 1986), but recently it has been recorded from the transition rainforest-steppe (41.2° S, 71.2° W, Ibargüengoytía *et al.*, 1997), overlapping with *L. pictus*, a typical rainforest lizard. The cycle of female *L. elongatus* from a Mendoza population (ca. 32.5° S, 69.3° W and 2700 m high) has been described (Ramírez Pinilla, 1992b) as annual and showing vitellogenesis from beginning of summer until end of spring. Females were noted to be gravid from late spring to late summer followed by a new cycle, without a period of rest. An annual male cycle has been described, for the same locality of Mendoza (Macola *et al.*, 1984; Ramírez Pinilla, 1992b). These results have the following problems: (1) authors do not differentiate adults from juveniles; (2) Macola *et al.* (1984) describe a rest period in summer and a "receso" (rest?) period in winter, while the same winter individuals are considered active (high testicular volumes) by Ramírez Pinilla (1992b); and (3) the latter author does not discuss the pregnant females caught in mid- and late summer (see Fig. 2, pp. 70).

The aim of this work is to describe the reproductive biology of *L. elongatus*, in order to increase the understanding of the effect of environment factors on the reproduction of *Liolaemus* lizards.

MATERIAL AND METHODS

COLLECTION OF SPECIMENS

Three set of specimens were used: Group A: $n = 39$, collected from October to March (1981 to 1984), in Nahuel Huapi and Lanín National Parks; Group B $n = 35$, collected from November to March (1993 to 1995), in San Carlos de Bariloche. Localities of groups A and B are situated between 39° to 41.5° S and 71.6° to 70.5° W, from 500 to 1800 m high. Specimens are deposited in the Centro Regional Universitario Bariloche of the Universidad Nacional del Comahue. Group C: $n = 130$, collected from December to January in Neuquén (1963

to 1973) and Mendoza Province (1961 to 1994). Localities are situated between 32° to 41.07° S and 66.52° to 71.97° W) and specimens are deposited in the Instituto de Biología Animal of the Universidad Nacional de Cuyo.

AUTOPSY PROCEDURES

Lizards were killed by intraperitoneal administration of sodic thiopental, fixed in 4% formaldehyde for 10 days (Groups A and C) or Bouin's solution (Group B) for 24 hr, and preserved in 70 % ethanol. Small lizards (SVL 23.1 to 29.66 mm), were not dissected.

The uteri were characterized by morphological observations into three categories: (1) Uterus type 1: folds, if present, are small, and never spread over all the uterus, similar to the thread-like oviduct typical of juveniles reported by van Wyk (1991); (2) Uterus type 2: medium size folds spread all over the uterus, indicative of the distended oviducts of adulthood *sensu* Vitt & Caldwell (1993), and generalized hypertrophy of the oviducts associated with vitellogenic recrudescence (Ramírez Pinilla, 1992a); and (3) Uterus type 3: similar to type 2 but conspicuously more stretched with bigger folds. This type seems to be analogous to the stretched oviducts (Flemming & van Wyk, 1992) and to the post-reproductive uterus (Ramírez Pinilla, 1992a), in both cases an indication of recent parturition.

Ovarian size was estimated as the diameter of the largest follicle, recorded with a vernier calliper on camera lucida schemes. For testicular size the antero-posterior diameter was used.

The maximum juvenile size was determined taking into account the size of the smallest female with ovulated oocytes or Uterus type 2 (Van Wyk, 1991; Mouton & Van Wyk, 1993), and the smallest male showing testicular growth during the breeding season (Vitt & Caldwell, 1993; Censky, 1995). Litter size was estimated by counting the number of ovulated oocytes or embryos in uterus.

DATA RECORDED

Capture dates were considered as days counted from 21 September, in order to consider a standard year starting the first day of spring (Southern Hemisphere), approximately when lizards become active.

The following data were recorded for each lizard: sex, gonadal size, snout-vent length (SVL), head length (HL), head width (HW) and width at vent (WAV). When needed, all original measures were transformed using natural logarithms to approximate multivariate normality and linear relationships, and corrected for SVL according to the following equation (Reichow *et al.*, 1991):

$$AM = OML - (RC \times (\ln SVL - \text{Mean}(\ln SVL)))$$

where AM = adjusted measurement; OML = original measurement logarithm; RC = regression coefficient between the logarithm of the character and the loga-

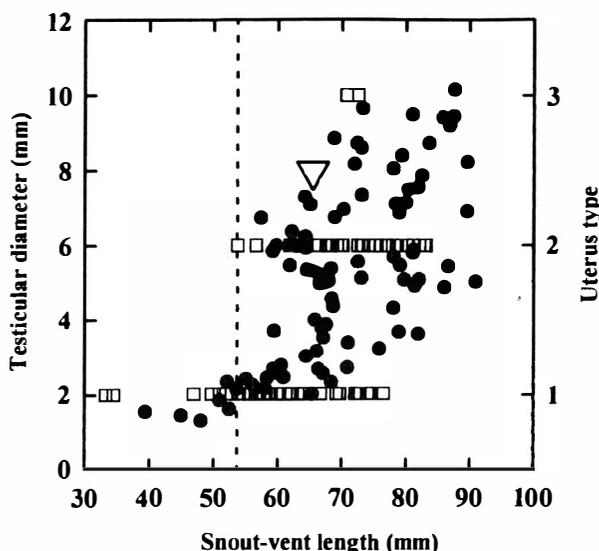


FIG. 1. Maximum juvenile size (SVL, vertical dashed line) in relation to the smallest gravid female (triangle), male testicular diameter (circles) and uterus type (squares).

rithm of SVL, $Mean(\ln SVL)$ = overall mean of SVL logarithm.

STATISTICAL ANALYSIS

Data were studied using analysis of variance (ANOVA), regression analysis, and the paired *t*-test. Normality and variance homogeneity assumptions were tested comparing predicted and observed frequencies by means of the Kolmogorov-Smirnov test, and by analysis of residuals or the Levene test, respectively. When normality or variance homogeneity assumptions did not hold, Mann-Whitney and Runs tests were used instead (Sokal & Rohlf, 1969; Norusis, 1986).

RESULTS

JUVENILE PERIOD, SEXUAL DIMORPHISM AND SEX RATIO

The smallest female found with ovulated oocytes in the uterus was 65.44 mm SVL whereas Uterus type 2 appears at 53.74 mm SVL. The smallest male showing testicular growth was 57.26 mm SVL. Thus the maximum juvenile size (SVL) was considered less than 53.74 mm (Figs. 1 and 2).

Juveniles were caught from mid spring to late autumn. Although juvenile SVL frequency was normal (Kolmogorov Smirnov test: $Z = 1.28, n = 30, P > 0.07$), grouping SVL less than and more than 37.5 mm shows the existence of two groups (Fig. 3; Runs test: $Z = -4.71, n = 30, P < 0.0001$).

Juvenile and adult lizards show different allometric relationships between the three recorded body measurements (head length, head width and width at vent) and SVL. Comparison of 95 % confidence intervals for slopes of adults and juveniles showed that head length grew slower than SVL in juveniles ($n = 30$), adult males

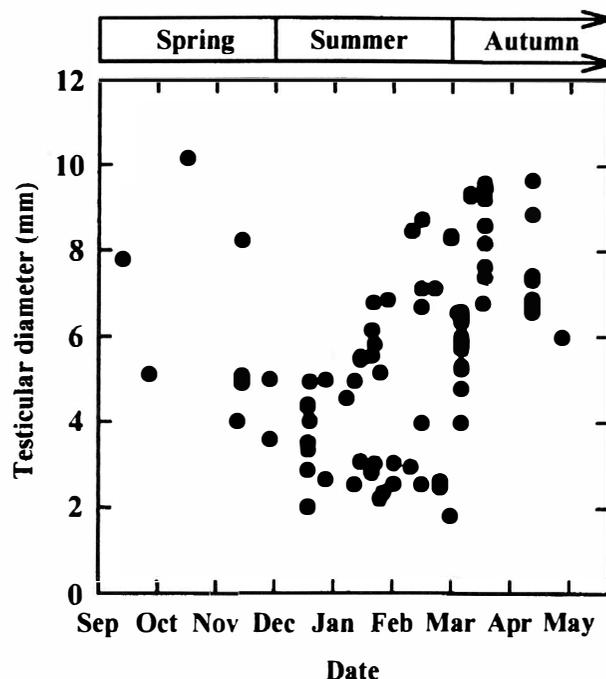


FIG. 2. Testicular diameter of adult males versus capture date.

($n = 84$), and females ($n = 87$). Particularly, the 95 % confidence interval for the slope was lower for juveniles than for adult males and females. At the same time, head width grew slower than SVL in juveniles ($n = 30$) and adult females ($n = 87$). In adult males, head width ($n = 84$) growth was isometric. Width at vent grew faster than SVL in juveniles ($n = 30$) and adult males ($n = 84$), while in adult females ($n = 87$) growth was isometric (Fig. 4).

SVL did not differ between adult males and females (Mann Whitney test: $n = 171, Z = 1.4708, P > 0.14$), but head length (Mann Whitney test: $n = 171, Z = 5.0935,$

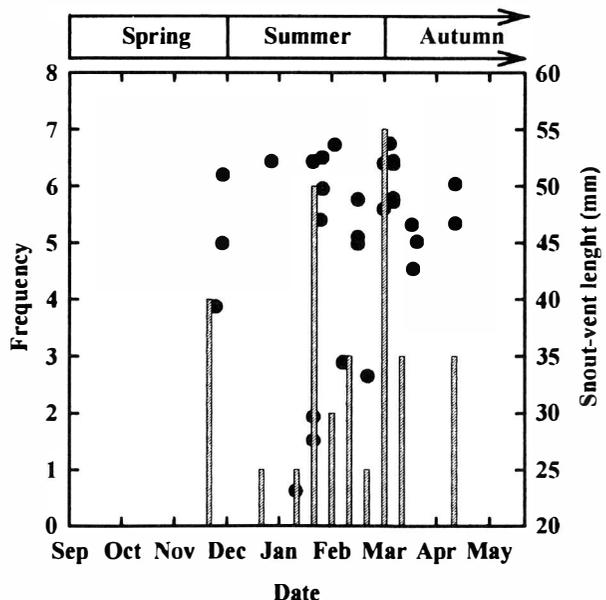


FIG. 3. Frequency (histogram) and SVL (circles) of juveniles versus capture date.

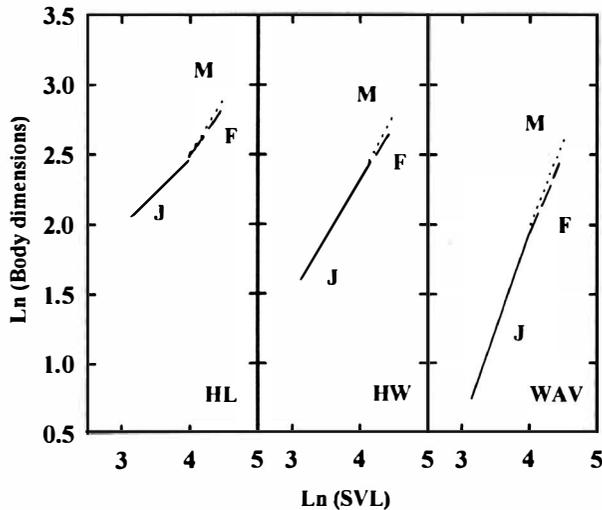


FIG. 4. Juvenile (J, solid line), adult male (M, dotted line), and adult female (F, dashed line) allometric relationship of head length, head width and width at vent with SVL. Regression lines are indicated.

$P < 0.0001$), head width (Mann Whitney test: $n=171$, $Z=6.4484$, $P < 0.0001$) and width at vent did (Mann Whitney test: $n=171$, $Z=6.2290$, $P < 0.0001$; adjusted measurements used in all tests). The three variables had greater values for males (Fig. 4).

Amongst all the specimens collected, the ratio of adult males to adult females was 0.97:1.

GONADS AND REPRODUCTIVE CYCLE

Adult Males. A slight difference was found between right and left testicular diameter ($t = 4.45$, $df = 83$, $P < 0.0001$), so values for the largest testicle (right) were used.

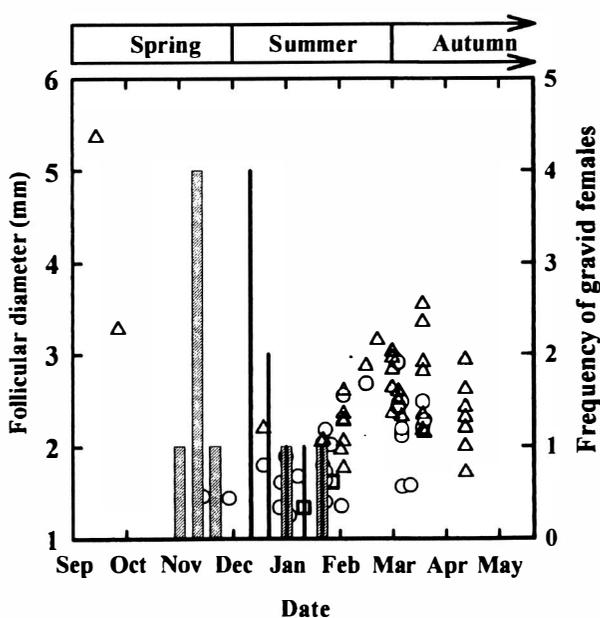


FIG. 5. Follicular diameter of adult females (circles: Uterus type 1, triangles: Uterus type 2 and squares: Uterus type 3) versus capture date. Frequency of gravid females, with early (dashed bars) and late developed embryos (black bars) are also indicated.

The relationship between testicular size and date of capture showed the biggest testicular size in mid-spring, a minimum in summer, and a clear gonadal recrudescence, reaching its peak value in autumn (Fig. 2). The relationship of Log (testicular size) with Log (SVL) was significant ($F = 30.46$, $df = 79$, $P < 0.0001$, Fig. 1) and showed positive allometry (95 % confidence interval for slope > 1).

Adult Females. Differences between right and left follicle diameter ($t = 0.75$, $df = 68$, $P > 0.456$) were not found. Average follicle diameter showed an isometric relationship with SVL ($F = 11.15$, $df = 66$, $P < 0.002$) and a linear relationship with date of capture ($F = 26.94$, $df = 64$, $P < 0.0001$). Gravid females and the two advanced vitellogenic females caught in spring were excluded from the analysis (Fig. 5).

The span from the time the first adult female was caught in summer, until the record of the highest follicular diameter in autumn, was 124 days, with the gonadal diameter ranging from 1.25 mm to 3.55 mm. The size of the smallest oocyte found in the uterus was 9.17 mm (uterine wall included).

Gravid females ($n=17$) were captured from late spring (3 December) to mid summer (9 February). It must be noted that early and advanced pregnancy both occur in mid-summer (Fig. 5). The first female found with Uterus type 3 was captured on 27 January.

Litter size ranged between three and seven foetuses, from females that varied between 65.44 and 82.38 mm SVL ($n=5$, other gravid females underwent extraction of some embryos previously to this study).

In summary, female cycles showed vitellogenesis in summer through winter with ovulation in the following spring. Females were gravid throughout late spring and summer, birth possibly taking place from mid-summer to autumn.

DISCUSSION

A clear assessment of adulthood is necessary to analyse reproductive cycles, differentiating non-reproductive adults from juveniles (van Wyk, 1991; Flemming & Van Wyk, 1992; Vitt & Carvalho, 1992; Mouton & van Wyk, 1993; Vitt & Caldwell, 1993; Flemming, 1994; Censky 1995; Ibarquengoytia & Cussac, 1996). In *L. elongatus*, yolk deposition is not conspicuous in preserved ovaries. Nevertheless, the appearance of pregnancy, Uterus type 2, and the increase of testicular growth allows the assessment of a common size for attaining adulthood in both sexes. The juvenile population shows two cohorts. Capture dates of the lower SVL group suggest that birth takes place in summer. Modal grouping of juveniles by SVL shows that, as in *L. pictus* (Ibarquengoytia & Cussac, 1996) and *Sceloporus occidentalis* (Sinervo & Adolph, 1994) adulthood would not be reached before one and a half years after birth.

We failed to record differences between adult male and female SVL and also between maximum juvenile size. As in *L. pictus* (Ibarquengoytia & Cussac, 1996), male *L. elongatus* have larger heads and wider tail bases than females. Adult male and female head shape

differs from that of juveniles. Sexual selection may account for such dimorphism (Mouton & van Wyk, 1993; Censky, 1995).

Data on male cycles suggests there is gonadal recrudescence from summer to autumn. Spring adults indicate a prolonged spermatogenetic period of one year. These events show high synchrony with the female cycle. On the basis of the analysis of follicular diameters, we postulate that in *L. elongatus* vitellogenesis begins in summer and continues until the following spring when, as the difference between follicular and oviductal oocyte size suggests, it is suddenly completed.

Callard *et al.* (1992), point out that vitellogenesis and pregnancy are two phenomena that are mutually exclusive for a viviparous squamate female. If this is the case, capture dates of vitellogenic and pregnant females should show a sequential pattern within the population. In *L. elongatus*, the simultaneous presence of females showing early pregnancy and females initiating vitellogenesis strongly suggests an overlapping situation (see Ibarquengoytia & Cussac, 1996). In the same way, the co-occurrence of adult females with low and high gonadal size suggests a biennial cycle (van Wyk, 1991; Ibarquengoytia & Cussac, 1996). These hypotheses imply the presence of both vitellogenic and non vitellogenic adult females during autumn and winter but, due to the cool and snowy winter, capture is normally not possible. On the other hand, both females with Uterus type 3 and the advanced pregnant females caught in summer, seem to be able to begin a new vitellogenic cycle in the same season. We propose that *L. elongatus* populations consist of annual cycles in males, and annual and biennial cycles in females. This plasticity in reproductive strategy could be one of the conditions that allow its range to encompass a wide range of steppe and cold montane environments. Causal relationships between reproductive timing and access to heat may be complex since environmental temperature also influences food availability, and this constrains reproduction (Hahn & Tinkle, 1965; Greenberg & Gist, 1985, Bonnet, Naulleau & Mauget, 1992). Fat bodies and gut content studies will be necessary to estimate the relative importance of each factor.

The reproductive cycle of *L. elongatus* closely resembles that of *L. gravenhorsti* (Leyton, Miranda & Bustos Obregón, 1980; Leyton, Morales & Bustos Obregón, 1977), but an important difference must be noted. Overlap between early pregnant and early vitellogenic *L. elongatus* females implies that individuals may be at different stages of the reproductive cycle within the same population (Cree & Guillette, 1995; Ibarquengoytia & Cussac, 1996). However, overlap between preovulatory and early pregnant *L. gravenhorsti* females does not obviate an annual cycle. Increasing plasticity of reproductive responses can be envisioned by comparing *L. gravenhorsti*, *L. elongatus* and *L. pictus* (Leyton, Miranda & Bustos Obregón, 1980; Ibarquengoytia & Cussac, 1996). Reproductive pat-

terns in these species appear to be correlated with their latitudinal and altitudinal distribution.

ACKNOWLEDGEMENTS

We wish to express our gratitude to José M. Cei and Raymond Laurent for their valuable assistance in clarifying the identification of some individuals and to Carmen Ubeda and Miguel Christie for the critical review of the manuscript. We also acknowledge the constructive and insightful comments of the two anonymous reviewers. This work was partially supported by Universidad Nacional del Comahue.

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Accepted: 10.6.97

SHORT NOTES

HERPETOLOGICAL JOURNAL, Vol. 8, pp. 107-110 (1998)

**NATURAL HISTORY OF
TROPIDURUS SPINULOSUS
(SQUAMATA: TROPIDURIDAE)
FROM THE DRY CHACO OF SALTA,
ARGENTINA**

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The genus *Tropidurus* is very complex and diverse, at least 44 recognized species are distributed in tropical and central South America (Rodrigues, 1987; Frost, 1992; Cei, 1993). *Tropidurus spinulosus* is a medium-sized lizard, inhabiting all of north-central Argentina and central Brazil. In Cordoba, Argentina, this lizard is observed on granitic boulders (Martori & Aùn, 1994), whereas in the dry chaco and cerrado habitats it is observed on tree trunks (Vitt, 1991; Colli, *et al.*, 1992; Lavilla *et al.*, 1995). *Tropidurus spinulosus* is very cryptic on tree bark.

Different aspects of the ecology of this species have previously been studied, including diet (Vitt, 1991; Colli *et al.*, 1992; Martori & Aùn, 1994), and it has been found to be mainly insectivorous. Only Colli *et al.* (1992) found plant material in *T. spinulosus* stomachs but the relative composition of fruits, flowers and somatic parts was not described. Flowers were part of the diet in three populations of *Tropidurus* species studied by Vitt (1991, 1993); Van Sluys (1993) found flowers, leaves and seeds in *T. itambere*. Vitt *et al.* (1996) commented on the presence of fruits in *T. hispidus* diet from Roraima (Brazil). Reproduction was studied by Vitt (1991) and Martori & Aùn (1994); only the latter work described the length of the reproductive cycle and the number of clutches per year, although both articles provided data on clutch characteristics. Thermal biology was described by Martori & Aùn (1994).

Vitt & Zani (1996) commented on the need to collect basic natural history data on neotropical lizards, as most life-history traits could be obtained from such data (e.g. Tinkle *et al.*, 1970; Dunham & Miles, 1985; Fitch, 1982). The aim of this study is to provide further data on the diet, reproduction, and thermal biology of *T. spinulosus* from the dry chaco of Argentina. The information obtained herein will then be compared to data of the same species from other localities, and to other *Tropidurus* species.

The study site is located on a private ranch called "Los Colorados" (24°35'S, 63°11'W), Salta, Argentina. The climate is characterized by a marked rainy season between October and April, during which more than 85% of the annual precipitation (530 mm) falls. Tem-

perature also varies seasonally, but in a less-pronounced cycle than rainfall, which is typical for temperate-subtropical climates (Bucher, 1980). The type of habitat corresponds to what Cabrera & Willink (1980) called the chacoan occidental district.

Lizards were studied during the spring-summer months between October 1995 and January 1997. *Tropidurus spinulosus* is active mainly during the warmer months, that is, from September through to March.

Sampling was performed in two plots of approximately 1 ha each, which lay within a total 10 000 hectares of the "Los Colorados" ranch. Lizards were collected by shooting with an air rifle, as the heights at which they were observed made other collection methods, such as noosing or pitfall trapping, difficult. After killing, specimens were fixed in 10% formaldehyde and then transferred to 75% ethanol. The sampling areas were therefore very small in relation to the total areas available to the lizards, and the trees from which samples were taken were observed to be recolonized by lizards within a few weeks. The sampling was therefore considered to have a negligible effect on lizard populations, particularly when related to the extensive loss of dry chaco habitat due to agricultural development. The material was deposited in the collection of the Instituto de Herpetología, Fundación Miguel Lillo (FML), Tucumán, Argentina.

Stomach contents and parasites were dissected out and analysed in the laboratory. The length and width of each prey item was measured with vernier calipers to the nearest 1 mm. Prey volume was estimated using the formula for a spheroid or a cylinder depending on the type of prey. Niche breadth was calculated using the reciprocal Simpson's measure following Vitt (1991, 1993). The first lizards to reach maturity were taken as the smallest male and female with evidence of reproductive activity; individuals smaller than these were considered to be juveniles. Reproductive stages were determined on the basis of enlarged (yolked) follicles and oviductal eggs in females, and enlarged testes and convoluted epididymides in the males. The number of enlarged follicles and oviductal eggs was used to estimate clutch size. Temperature data were obtained using a thermocouple within 30 seconds of shooting the individual, and air temperature was taken 1-3 cm above the ground; substrate temperature was taken 1 cm into the soil.

One hundred and thirty-eight lizards were captured at the study site, 130 of which (94%) were captured on tree trunks. Diet data of *T. spinulosus* were obtained from 92 individuals (mean SVL = 98.11 mm; SD = 19.24; range = 37.49-131.76). Mature males were larger (mean = 107.22 mm; SD = 16.33; range = 75.7-139.8; $n = 50$) than mature females (mean = 94.09 mm; SD = 7.98; range = 80.34-110.15; $n = 35$), exhibited larger dorsal spines and were more brightly coloured than females.

TABLE 1. Diet composition of *T. spinulosus*. No. lizards indicates the number of lizards containing each prey category; No. items is the number of items corresponding to each category; Volume is the total volume (mm³) found for each category. % represents percentages of the total sample.

Prey type	No. lizards	% lizards	No. items	% items	Volume	% Volume
Orthoptera	14	15.22	15	0.54	5413.93	2.79
Aerididae	12	13.04	13	0.46		
Gryllidae	2	2.17	2	0.07		
Hemiptera	12	13.04	17	0.61	11965.32	6.16
Pentatomidae	8	8.70	9	0.32		
Lygaeidae	4	4.35	8	0.29		
Coleoptera	67	72.83	154	5.51	43678.63	22.49
Scarabidae-Carabidae	43	46.74	77	2.75		
Scarabidae	11	11.96	17	0.61		
Coccinellidae	7	7.61	37	1.32		
Staphylinidae	6	6.52	7	0.25		
Curculionidae	4	4.35	7	0.25		
Cerambycidae	3	3.26	3	0.11		
Tenebrionidae	3	3.26	4	0.14		
Lampyridae	1	1.09	2	0.07		
Formicidae	75	81.52	1594	56.99	39080.64	20.12
Other Hymenoptera	43	46.74	167	5.97	22688.61	12.40
Apidae	35	38.04	154	5.51	19853.67	10.94
<i>Apis</i>	21	22.83	56	2.00		
<i>Melipona</i>	20	21.74	98	3.50		
Vespididae-Sphecidae	10	10.87	13	0.46	2834.94	1.46
Lepidoptera	3	3.26	24	0.86	24651.90	12.69
Diptera	8	8.70	14	0.50	1139.12	0.59
Araneae	10	10.87	12	0.43	10951.56	5.64
Larvae	61	66.30	155	5.54	16516.81	8.50
Coleoptera	39	42.39	117	4.18		
Lepidoptera	18	19.57	23	0.82		
Unidentified larvae	12	13.04	15	0.54		
Blattaria	12	13.04	18	0.64	8143.53	4.19
Homoptera	8	8.70	571	20.41	5423.67	2.79
Cicadelidae	1	1.09	560	20.02		
Cicadidae	7	7.61	11	0.39		
Pseudoescorpionida	7	7.61	8	0.29	154.93	0.08
Isoptera	6	6.52	8	0.29	282.05	0.15
Myriapoda (Julida)	4	4.35	4	0.14	757.77	0.39
Unidentified insects	10	10.87	10	0.36	3387.12	1.74
Fruits	22	23.91	26	0.93		
<i>Ceigis</i>	13	14.13	17	0.61		
<i>Ziziphus</i>	5	5.43	5	0.18		
Other fruits	4	4.35	4	0.14		
TOTAL	92		2797		194239.59	

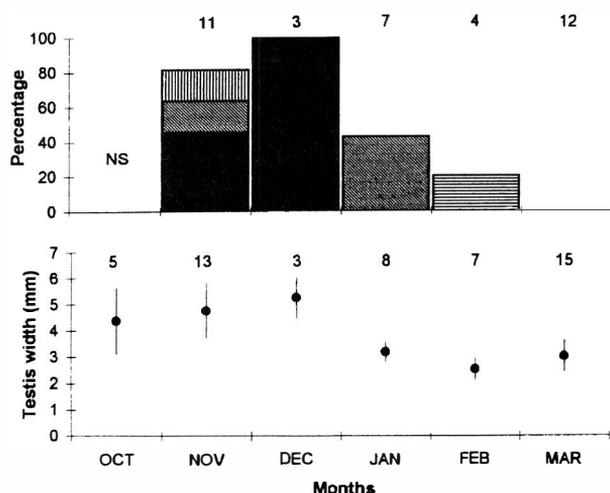


FIG. 1. Reproductive events of *Tropidurus spinulosus*. Top: filled bars represent enlarged follicles, hatched bars represent oviductal eggs, vertical lines represent simultaneous oviductal eggs and enlarged follicles; horizontal lines represent corpora lutea. Below: dots and lines represent mean testis width \pm 1SD, respectively. In both cases data are grouped by month and upper numbers represent sample size, NS= no sample.

Tropidurus spinulosus in the dry chaco of Argentina feeds mainly on ants, beetles, coleopteran and lepidopteran larvae, and bees (Table 1). Fruits are also present in the diet; 22 out of 92 individuals contained entire mature fruits of *Ceitis tala* and *Ziziphus mistol*, that are common in the study area and that fall on the ground when mature. Adult lepidopterans were abundant in volume, but not in number or occurrence. Lizards were observed feeding while they were vertically perched on tree trunks.

From 2766 identified prey, 72.74 % were active insects, whereas 764 prey (560 Cicadellidae corresponded to a single stomach) were motionless or very slow-moving arthropods (Blattaria, Homoptera, Pseudoscorpionida, Isoptera and Myriapoda) and larvae. Only one specimen was found with exclusively non-mobile prey. Within each stomach, more than one species of ant, and at least two castes (workers and soldiers), were observed. Mean number of prey categories per stomach was 4.29 (SD = 2.01; range = 1-12), with only five individuals containing a single prey category. Number of prey did not vary significantly with SVL. Average prey length was 9.86 mm (SD=5.65; range = 1.95-34.07 mm; $n = 358$). No significant relationship ($P > 0.05$) was found between mean prey length or maximum prey length and lizard SVL, but total volume increased with SVL ($r = 0.382$, $n = 87$, $P < 0.05$).

Mean maximum prey volume was 419.57 mm³ (SD = 416.56; $n = 82$). Diet niche breadth was 2.61 by prey number and 7.7 by prey volume.

One stomach contained one fore-limb from a conspecific. Two stomachs contained bird egg shell, and five stomachs were totally empty.

Females were reproductive from November to January (Fig. 1). Mean clutch size was 5.0 (range = 3-7; $n = 17$) and positively correlated with female SVL ($r =$

0.48; $P < 0.05$; $n = 17$). More than one clutch per year could be laid according to the simultaneous presence of enlarged follicles and oviductal eggs in some females. Males were reproductively active from October to December, and in January testis width decreased considerably (Fig. 1).

Body temperatures ranged from 29.2°C to 37.8°C (mean = 34.22°C; SD = 1.83; $n = 37$), and was higher than air and substrate temperature (Air: mean = 29.33°C, range = 24.3-34.5; SD = 2.9; $n = 31$. Substrate: mean = 29.36°C; range = 22.1-35.5; SD = 3.54, $n = 31$). Body temperature was positively correlated with both air and substrate temperature ($r = 0.447$, $P < 0.014$, $n = 31$; $r = 0.42$, $P < 0.02$, $n = 31$, respectively).

Tropidurus spinulosus from dry chaco feeds on a variety of arthropods, but primarily on ants, beetles, larvae and bees. Mobile prey (active insects) are more abundant in the diet, as expected for a sit-and-wait forager. Interestingly, about 25% of the individuals contained fruits in their stomachs. Flowers and plant matter were recorded for the diet of other *Tropidurus* species (Vitt, 1991; Van Sluys, 1993). Colli *et al.* (1992) found almost 10% of the diet was plant matter in *T. spinulosus* from Mato Grosso (Brazil), but fruits were only mentioned by Vitt *et al.* (1996) in *T. hispidus* from Roraima (Brazil). Another distinguishable aspect in this population was the role of bees in the diet. Bees are abundant and use tree holes in the study area, and some *T. spinulosus* were observed feeding around tree holes, presumably on bees or wasps. Data from other localities (Vitt, 1991; Colli *et al.*, 1992; Martori & Aùn, 1994) are consistent with the results obtained here with respect to the dominance of prey categories; ants, beetles, larvae, and non-ant hymenopterans are the main sources of food for *T. spinulosus*; the differences are given by the importance of fruits and bees.

In the dry Chaco, *T. spinulosus* eat larger prey and have a wider niche breadth than Brazilian populations (Vitt, 1991; Colli *et al.*, 1992). *Tropidurus spinulosus* in the Chaco is 10 mm larger in mean SVL than in Brazilian localities. The size of ants could explain the differences observed in the diet better than the SVL. The number of different prey categories is also higher than in the other localities studied, reaching 16 prey categories. Mean ant length and volume in the diet of *T. spinulosus* (6.04 mm and 38.34 mm³) is larger than the values obtained for total prey in the studies by Vitt (1991) and Colli *et al.* (1992).

Reproductive characteristics in *T. spinulosus* are similar to other *Tropidurus* species (Vitt & Goldberg, 1983; Vitt, 1991, 1993; Van Sluys, 1993; Cruz, in press).

In the dry chaco *T. spinulosus* reproduce seasonally, with a relatively low clutch mass, and more than one clutch per cycle (Cruz *et al.*, in press). In Cordoba only one clutch is laid (Martori & Aùn, 1994). This difference could be related to the degree of arboreality of the Chaco population; smaller clutches (low RCM) are easier to carry by an arboreal individual, and by laying

a second clutch, the differences in individual clutch characteristics could be less pronounced in relation to that of Cordoba population. Furthermore, the higher temperatures and the greater duration of favourable climatic conditions in Salta (where lizards could be observed for a longer period than in Cordoba), could also favour a second clutch.

Tropidurus spinulosus body temperatures were closer to those of *T. torquatus*, *T. itambere*, *T. oreadicus* and *T. etheridgei* (Bergallo & Rocha, 1993; Vitt, 1993; Van Sluys, 1992; Cruz *et al.*, unpublished data), than to the population from Cordoba belonging to the same species (Martori & Aùn, 1994). This may reflect air and substrate temperatures, and it may also be due to the fact that *Tropidurus* species are thermoconformers, possibly as a result of selection of particular thermic sites along their activity range (Huey & Slatkin, 1976; Espinoza & Tracy, in press).

Tropidurus spinulosus show plasticity in their habits, and they can be arboreal or riparian depending on where they are found. In Argentina this species has a distinct reproductive cycle. More than one clutch may be laid in Salta, while in Cordoba a single clutch is laid per cycle. Myrmecophagy seems to be characteristic of *T. spinulosus*, but in the dry chaco bees and fruit are also conspicuous in the diet.

Acknowledgements. G. J. Scrocchi, G. Leynaud, O. Varela and M. Beleizin helped in field work. L. Ann, R. Espinoza, L. A. Fitzgerald, R. F. Laurent, R. Martori, M. Halloy, G. J. Scrocchi, L. J. Vitt and two anonymous reviewers provided useful comments on the manuscript. G. Claps helped with insect identification. Ing. Carlos Saravia Toledo provided logistic support and allowed me to work on his property. PID No.3722/92 from CONICET financed part of this study.

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HERPETOLOGICAL JOURNAL, Vol. 8, pp. 111-113 (1998)

ANURAN ASSEMBLAGES IN CRASTO FOREST PONDS (SERGIPE STATE, BRAZIL): COMPARATIVE STRUCTURE AND CALLING ACTIVITY PATTERNS

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Individual anuran species are often restricted to a particular aquatic habitat (Heyer *et al.*, 1975; Smith, 1983; Diaz-Paniagua, 1990; Gascon, 1991; Rossa-Feres & Jim, 1994; Zimmerman & Simberloff, 1996). The preference of a species for a particular type of breeding habitat must reflect differential fitness of that species in the various habitats available to it (Grubb, 1972). Abiotic and biotic factors may determine the use of specific kinds of aquatic habitats by frogs with larval stages (Heyer *et al.*, 1975). Hydroperiod is particularly important in determining the survival of larval amphibians because it governs not only the amount of time that larvae will have to complete metamorphosis but also the way in which competition and predation affect the composition and trophic interactions of the community (see references in Dodd, 1993; Rowe & Dunson, 1995).

Among anurans, the most common and phylogenetically widespread site of oviposition is in free water - standing or flowing, permanent or temporary. Aquatic eggs and tadpoles are characteristic of most hylids. On the other hand, the construction of a foam nest on the surface of the water in ponds is characteristic of most leptodactyline leptodactylids (Duellman & Trueb, 1986). Heyer *et al.* (1975) suggested that ponds susceptible to drying may be typical habitats for certain frog species, such as those in which the tadpoles are more resistant to desiccation. Foam nests provide protection against desiccation. In ponds in which the water level fluctuates, many foam nests may be out of water for a day or two, but the interior of the nest remains moist. Thus recently hatched tadpoles may remain in the nest for a short period until the water level rises (Duellman & Trueb, 1986).

The objective of the present study was to compare nocturnal anuran assemblages at two adjacent aquatic breeding sites with different hydroperiods. Comparisons include species composition, predominant habitat (arboreal versus terrestrial) occupied by each assemblage as a whole, calling activity patterns and reproductive modes.

The natural ponds studied are in Crasto Forest (11°20'S; 37°25'W), a large, contiguous tract of remnant Atlantic Forest in the State of Sergipe (Sta. Luzia do Itanhý), north-eastern Brazil. Gururema is a permanent pond (70 m maximum length and 1.8 m maximum depth) on the edge of the forest and is located approximately 1350 m from Mangueira Grande, a temporary pond (30 m maximum length and 0.8 m maximum depth) also situated on the edge of the forest. About half of the margins of both ponds is therefore surrounded by medium or large trees and shrubs (especially Leguminosae, Malpighiaceae, Myrtaceae, and Verbenaceae) whereas the other half is surrounded by low (Cyperaceae, Gramineae, and Verbenaceae) or no vegetation. Within the Gururema pond, near the western edge, occurs an "islet" formed by emergent macrophytes. *Utricularia inflata* (Lentibulariaceae) covers much of the remaining surface area (Souza & Couto, 1997). The permanent pond contained water for the duration of the study, but was shallow during the driest months. The temporary pond contained water only from 1 July 1994 to mid-November 1994.

Field work was carried out from 1 July 1994 until 31 July 1995. Heavy rains occurred from July-October 1994 (569.5 mm) and from April-July 1995 (904.4 mm), and the dry season occurred from November 1994-March 1995 (192 mm). Data were collected during two visits per month to the study area. Observations were made from 1700 to 2200 hr or later. Calling males were counted along the margins of the ponds, aurally and/or visually. Four frequencies of calling males per species were discerned: (1) up to 5 individuals; (2) 5 to 10 individuals; (3) 10 to 50 individuals; and (4) 50 or more synchronously calling males in the pond (based on Aichinger, 1987). Amplexus and oviposition sites were only recorded for some of the species in the study area (*Hyla minuta*, *Scinax eurydice*, *S. gr. rubra*, *S. x-signata*, *Physalaemus cuvieri* and *P. kroyeri*). Amplexus and oviposition sites of other species were observed in other study areas by Arzabe (1991), Arzabe & Almeida (1997) and Arzabe (unpublished manuscript). Details of the techniques used and special considerations were described by Scott & Woodward (1994). As no other research about the anurans of Sergipe State was known to us, and basic questions regarding the distribution and taxonomic data of Atlantic Forest frogs remain unresolved, adult voucher specimens were deposited in the Museu Nacional, Rio de Janeiro, and in the Department of Biology, Universidade Federal de Sergipe.

A total of 17 species belonging to three families (Hylidae, Leptodactylidae, and Microhylidae) were recorded calling. Eleven species were found at each breeding site (see Table 1). Five species occurred at both the permanent and temporary ponds: *Hyla branneri*, *H. minuta*, *Scinax eurydice*, *S. gr. rubra*, and *Scinax x-signata*.

Most species in herpetofaunal assemblages in Neotropical rainforests can be categorized as terrestrial

TABLE 1. Calling patterns, maximum number of synchronously calling males per species, reproductive modes, monthly rainfall (mm), water supply and number of species calling each month in the temporary and in the permanent ponds at Crasto Forest, from 1 July 1994 to 31 July 1995. No. males: maximum number of synchronously calling males during the study period; Rep. mode: reproductive mode according to Duellman & Trueb (1986).

SPECIES	NO. MALES	REP. MODE	MONTHS												
			J	A	S	O	N	D	J	F	M	A	M	J	J
TEMPORARY POND:															
<i>Hyla minuta</i>	>50	1	+	+	+	+	-	-	-	-	-	-	-	-	-
<i>Scinax gr. rubra</i>	10-50	1	+	+	+	+	-	-	-	-	-	-	-	-	-
<i>Hyla branneri</i>	>50	1	-	+	+	+	-	-	-	-	-	-	-	-	-
<i>Scinax x-signata</i>	10-50	1	+	-	+	-	-	-	-	-	-	-	-	-	-
<i>Physalaemus kroyeri</i>	10-50	8	+	-	+	-	-	-	-	-	-	-	-	-	-
<i>Physalaemus cuvieri</i>	10-50	8	+	-	-	-	+	-	-	-	-	-	-	-	-
<i>Scinax eurydice</i>	10-50	1	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Leptodactylus labyrinthicus</i>	≤5	21	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Pseudopaludicola gr. falcipes</i>	>50	1	+	-	-	-	-	-	-	-	-	-	-	-	-
<i>Leptodactylus troglodytes</i>	10-50	21	+	-	-	-	-	-	-	-	-	+	+	-	-
<i>Leptodactylus spixii</i>	10-50	21	-	-	-	-	-	-	-	-	-	+	+	+	-
PERMANENT POND:															
<i>Hyla albomarginata</i>	5-10	1	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Hyla branneri</i>	>50	1	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Hyla faber</i>	5-10	3	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Hyla minuta</i>	>50	1	+	+	+	+	+	+	+	+	+	+	+	+	+
<i>Scinax gr. rubra</i>	>50	1	+	+	+	+	+	+	+	+	+	-	+	+	+
<i>Scinax x-signata</i>	10-50	1	+	+	-	-	+	-	-	-	+	+	+	+	+
<i>Hyla elegans</i>	10-50	1	+	+	+	+	-	-	-	-	-	+	+	-	-
<i>Scinax eurydice</i>	>50	1	+	+	+	-	-	-	-	-	-	-	+	+	+
<i>Scinax cf. aurata</i>	≤5	1	+	+	+	+	-	-	-	-	-	-	-	-	-
<i>Leptodactylus macrosternum</i>	10-50	8	-	-	-	-	-	-	-	-	-	+	-	-	-
<i>Dermatonotus muelleri</i>	≤5	1	-	-	-	-	-	-	-	-	-	-	+	-	-
Rainfall (mm)			307	49	131	82	9	45	19	72	47	356	189	157	202
Temporary pond: water supply			+	+	+	+	+	-	-	-	-	-	-	-	-
Temporary pond: species calling			9	3	5	3	1	0	0	0	0	2	2	1	0
Permanent pond: water supply			+	+	+	+	+	+	+	+	+	+	+	+	+
Permanent pond: species calling			9	9	8	7	6	5	5	5	6	7	9	7	7

(including fossorial, leaf litter, and aquatic margin) or arboreal (bushes, tree trunks, and tree limbs) (Duellman, 1990). Among the anurans recorded in this study, nine are arboreal (hylids) and eight are terrestrial (leptodactylids and one microhylid). At the temporary pond we recorded terrestrial ($n=6$) and arboreal species ($n=5$) in almost equal proportions whereas in the permanent pond arboreal species ($n=9$) predominated. In the temporary pond calling activity was markedly seasonal, whereas in the permanent pond arboreal species such as *Hyla albomarginata*, *H. branneri*, *H. faber*, and *H. minuta* showed annual calling activity patterns (Table 1), with few calling males during the driest months. The annual calling activity pattern observed in the permanent pond probably resulted from the interrelationship between water supply and the potential of the arboreal environment (occupied by the majority of the species) to ameliorate the harsh effects of the wet-dry climate. Calling in frogs does not necessarily mean breeding (see Scott & Woodward, 1994), and observations of more explicit indicators, such as amplexus, egg masses or larvae, are needed to confirm annual reproductive activity.

Four reproductive modes (according to Duellman & Trueb, 1986) were associated with the species observed (see Table 1). Egg-deposition and larval development directly in water were characteristic of the majority of the anurans recorded in the permanent pond, whereas eggs in foam nests were characteristic of approximately 50% of the species observed in the temporary pond (*Leptodactylus labyrinthicus*, *L. spixii*, *L. troglodytes*, *Physalaemus cuvieri*, and *P. kroyeri*). Eggs and tadpoles in foam nests are protected during frequent filling/drying cycles of temporary ponds (see Heyer, 1969). On the other hand, the unstable hydroperiod of these breeding sites, especially during the critical first rains, is a limiting factor restricting the presence of species that deposit their eggs directly in water. Alternatively, these species may breed in these habitats during heavy and continuous rains or when these sites fill with rainwater and resemble permanent habitats (see Aichinger, 1987; Gascon, 1991).

The hydroperiod of temporary ponds is highly variable, depending upon elevation, basin characteristics, and rainfall patterns (Means, 1990). Some ponds may fill and dry on an annual basis whereas others may con-

tain water only in the wettest years (see LaClaire, 1995). Therefore, frogs may not breed in a specific pond every year. During the heavy rains in 1994 when the temporary pond was filled with water, we recorded up to nine synchronously calling species at each breeding site. On the other hand, during the heavy rains in 1995, the temporary pond remained without water and only two leptodactylids, both with terrestrial foam nests (see Arzabe & Almeida, 1997), were heard calling. In contrast to the temporary pond, the permanent pond once again had up to nine species calling synchronously (Table 1).

Our results showed that the composition, reproductive modes, and calling activity patterns differed among the two anuran assemblages and we suggest that these differences are particularly associated with the different annual hydrological cycles of the breeding sites. As suggested for wetland plant communities (Mitsch & Gosselink, 1986 in LaClaire, 1995), hydroperiod may be the major factor influencing and maintaining assemblages of anurans in temporary ponds.

Acknowledgements. We thank Drs. A.J. Cardoso (in memoriam), A. V. Alcântara, C. Gascon, C. F. B. Haddad, and A. Langguth for reviewing earlier drafts of the manuscript and offering helpful suggestions. Important corrections and helpful comments were made by Dr C. K. Dodd Jr. and by an anonymous reviewer. M. F. L. de Souza helped us in identifying trees and shrubs. C. Arzabe especially gives thanks for the encouragement and generous support provided by E. C. G. Couto and A.V. Alcântara from the Universidade Federal de Sergipe and M. C. de Sousa from the Universidade Tiradentes. CNPq provided grants to C. X. de Carvalho and M. A. Goes Costa.

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BOOK REVIEWS

Snakes. The Evolution of Mystery in Nature. Harry W. Greene. (1997). 364 pp. University of California Press, Berkeley. \$45.00 (cloth).

Snakes are difficult animals to get to know well. With a few exceptions, they are by nature solitary, secretive, and mysterious creatures. Unquestionably, snakes hold a unique fascination for people in general yet our knowledge of them is dominated by a few species while the vast majority of snakes may only be known from pickled specimens in museums. However, things are changing. More people are studying snakes in their natural habitat, and new techniques such as radio telemetry and molecular analysis are revealing the secrets of snakes in unprecedented detail. Harry Greene has been at the forefront of this investigation, and this book presents a comprehensive summary of the most recent developments in our knowledge.

The book has achieved a difficult balance, being beautiful to look at and easy to read while still being packed with meticulously catalogued information reflecting the latest scientific knowledge. The quality of Greene's scholarship and the clarity of his writing, together with the sheer beauty of the Fogdens' photographs (which are plentifully distributed throughout and give rare glimpses of snakes in action) have combined to produce a remarkable book. It is even more remarkable for retailing at a very reasonable price.

The book is divided into three parts. The first (*Lifestyles*) covers general topics in snake biology such as anatomy and feeding, social behaviour and reproduction. The second (*Diversity*), covers the main groups of snakes, not neglecting the small and insignificant. The final part is a synthesis, covering evolution and biogeography as well as the rich topic of man's continuing fascination with snakes. All this is backed up with more than 800 references as well as notes on sources for each chapter, with an appendix which covers the essentials of systematics and evolutionary inference for beginners.

The main text is interspersed with special topics, double-page inserts which cover a variety of areas, from the evolution of pits and rattles to morphological adaptations for defence in cobras. In these, Harry Greene shows clearly that in spite of the growing volume of work being done on snakes today, the mystery is very much still present. While others may present the accepted explanations for these phenomena uncritically, he is not afraid to speculate and frequently presents alternative, perhaps unconventional, ways of thinking about them. In some cases these appears a little bizarre; for example, when he suggests that human attitudes towards cobras may have influenced the evolution of their hood patterns, noting that the only

cobras with hood markings are found in areas where they are sometimes associated with religious beliefs. However, he also adds that the markings may simply enhance the defensive role of the hood!

Similarly, he questions the conventional view of the evolution of the pit organ of crotalines as an adaptation for prey location. He suggests that, as a result of the propensity of crotalines to exhibit brood-guarding behaviour, it may instead be critical for assessing the size and shape of an adversary at night. Differences between the defensive gape of *Atheris* (a true viper) and pit vipers (the former gape with their fangs extended, the latter with them retracted, allowing the pits to "see") and the predominately camouflage colour patterns of pit vipers are also brought in to underline the importance of defence. This example illustrates one of the strengths of Harry Greene's book: it is a true synthesis, cutting across narrow scientific specialisms. It also vividly communicates the transparent sense of wonder and the almost unscientific passion and excitement with which he continues to pursue the mysteries that snakes represent.

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Czech Recent and Fossil Amphibians and Reptiles. An Atlas and Field Guide. Petr Nečas, David Modry, and Vít Zavadil. (1997). 94 pp. Edition Chimaira: Frankfurt am Main.

Books on the amphibians and reptiles of the former Czechoslovakia, including the present-day Czech Republic, have usually been published in Czech (with occasional papers in German). This has made the literature relatively inaccessible to the majority of herpetologists throughout the world due to the obvious language barrier (e.g. Hrabě *et al.*, 1973; Baruš & Oliva, 1992a,b). This booklet aims to fill this gap. It is the first overview of Czech amphibians and reptiles published in English, which makes it usable by a wide audience, not only in the Czech Republic but also abroad.

The book is issued on the occasion of the Third World Congress of Herpetology (Prague, 2-10 August 1997) and aims to summarize current knowledge of the systematics and distribution of Czech amphibian and reptile species, with brief information on their biology and conservation. In addition to the principle authors, many other prominent herpetologists contribute to the book, both from within and outside the Czech Republic.

A brief account of the history of Czech herpetology introduces many interesting but poorly known works from the XVIII-XIX centuries, as well as up-to-date studies of the local reptiles and amphibians. The chapter ends with a list of numerous professional and amateur herpetological societies in the current Czech Republic, which reveals a considerable interest by

Czech people in amphibians and reptiles. The next chapter contains a description of main threats and measures for conservation of Czech herpetofauna, both at national and international levels. In this country, as in the majority of others, anthropogenic factors pose the main threat to amphibians and reptiles. The following chapter is dedicated to palaeontology. Fossil amphibians are known from Paleozoic and Cenozoic deposits, and reptiles from the Paleozoic and Mesozoic. In contrast to the amphibians, fossil reptiles are rare in the Czech Republic. There are detailed lists of localities and species but, unfortunately, there is no attempt to link fossil and recent amphibian and reptile faunas. Although it is very difficult to make such reconstructions, such historical perspectives are often of considerable interest to those studying the herpetofauna of the Czech Republic. However, palaeoclimatic data are not discussed.

Accounts of recent species of amphibians and reptiles occupy the main part of book: seven salamanders, 13 frogs and toads, one turtle, four lizards, and five snakes. Each species account is subdivided in a standard way; scientific name of species; common names (in five languages); systematics; morphological description (of adults and larvae); general distribution (in European countries and the Czech Republic); habitat (including altitude); notes on biology (included activity cycles, reproduction, development, and feeding); and conservation status. This information is presented in a way that is readily accessible to both the amateur herpetologist as well as the specialist. Sometimes, however, such data are too superficial (e.g., "the diet consists of terrestrial invertebrates") and not particularly informative. It would be better to provide precise information (e.g. on prey taxa) where this is available for different species. In order to save space, many terms from morphology and geography, as well as linguistic information and months, are given in abbreviated form.

Each species account is accompanied by a distribution map and excellent colour photographs of animals and their important external features. Indeed, each species is illustrated by several photographs, which gives an impression of variability in form, key characters, and life history. Some photographs, such as amplexus in albino *Rana lessonae* are unique. However, pictures on pages 67 and 68 seem to be confused: in contrast to the figure captions, fig. a on p. 67 is *R. esculenta*, and fig. a on p. 68 is *R. ridibunda*.

I hope that the book will attract interest from many herpetologists, and not only those working with European amphibians and reptiles. Quality of printing is quite high - a good start for "Chimaira", a relatively new publishing house in herpetology.

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- Sergius L. Kuzmin
Russian Academy of Sciences,
- Morphologic and Genetic Studies of the European Plethodontid Salamanders: Taxonomic Inferences (Genus: Hydromantes)*. B. Lanza, V. Caputo, G. Nascetti & L. Bullini. (1995). 366 pp. Museo Regionale di Scienze Naturali Torino, Monografie XVI, Torino. Lire 150.000.
- The European lungless salamanders are an enigmatic group of amphibians. Well over half of all salamanders belong to the family Plethodontidae, and they have undergone a vast radiation in the New World. In Europe, however, we have a paltry seven species, which occupy a relict distribution in northern Italy, south-east France and Sardinia. Theories abound as to how and why these cryptic animals have become so restricted in Europe, and this book provides a succinct account of the current debate in this area. No less confusing is the nomenclature of the genus. In the 1980's the senior author of this book suggested that the European lungless salamanders warranted a full genus of their own, distinct from their North American relatives, and *Speleomantes* was subsequently adopted by many, but by no means all, authors. As the most comprehensive treatise on these salamanders published to date, this book probably settles the matter, by reverting to the older *Hydromantes*.
- The book is presented as an extended scientific paper. A brief introduction to the family and genus is followed by a key to the species, and then a methods section describing the morphological and electrophoretic techniques used in the subsequent descriptions and analyses. The bulk of the text is then taken up with a description of the taxonomy of each of the seven species, encompassing a diagnosis, description, blood characters, karyotype, distribution, morphology, genetics, subspecies, and history of propagation (describing biogeography rather than captive breeding!). The morphological and genetic data are presented in extensive tables, many of which are several pages long. There is also a comprehensive appendix, giving precise locality data and maps, and an extensive bibliography.
- The Museo Regionale di Scienze Naturali in Turin is rapidly establishing a reputation for producing immaculately presented monographs and this volume follows in this tradition. Excellent colour photographs complement the painstakingly detailed text, and the fact that this volume has been published in English should ensure a wide readership.
- Richard Griffiths
University of Kent

THE HERPETOLOGICAL JOURNAL

INSTRUCTIONS TO AUTHORS

(revised January 1998)

1. The *Herpetological Journal* publishes a range of features concerned with reptile and amphibian biology. These include: *Full Papers* (no length limit); *Reviews* and *Mini-reviews* (generally solicited by a member of the editorial board); *Short Notes*; controversies, under *Forum* (details available from the Editor); and *Book Reviews*. Faunistic lists, letters and results of general surveys are not published unless they shed light on herpetological problems of wider significance. Authors should bear in mind that the *Herpetological Journal* is read by a wide range of herpetologists from different scientific disciplines. The work should therefore appeal to a general herpetological audience and have a solid grounding in natural history.
2. Three copies of all submissions, and illustrations, should be sent to the Editor. All papers will be subject to peer review by at least two referees. Authors are invited to suggest the names of up to three referees, although the editor may choose alternative referees to those suggested. Papers will be judged on the basis of the reports supplied by referees, scientific rigour, and the degree of general interest in the subject matter. The Editor's decision will be final.
3. Authors should consult a recent issue of the Journal regarding style. Papers should be concise with the minimum number of tables and illustrations. They should be written in English and spelling should be that of the *Oxford English Dictionary*. Papers should be typed or produced on a good-quality printer (at least near-letter quality, avoid worn ribbons), and double-spaced with wide margins all round. The journal is typeset direct from the author's computer diskette, so all manuscripts should be prepared using a wordprocessor (preferably on a PC-compatible microcomputer). It is not necessary to submit a computer diskette with the initial manuscript, but this will be required in the event of the manuscript being accepted for publication.
4. For all papers the title page should contain only the following: title of paper; name(s) of the author(s); address of the Institution where the work was done; a running title of 5 words or less, and no more than 5 keywords for abstracting purposes. The text of the paper should begin on page 2 and be produced in the following order: Abstract, Text, Acknowledgements, References, Appendices. Full papers and reviews should have the main text divided into sections. The first subhead will be centred in capitals, the second shouldered in lower case, and the third run on in italics. Footnotes are not permitted. *Short Notes* (generally less than six manuscript pages and accompanied by a single data set) should be produced as continuous text.
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9. Final acceptance of a paper will depend upon the production by the author of a typescript, illustrations and computer diskette ready for the press. However, every assistance will be given to amateur herpetologists to prepare papers for publication.
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