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## MINI-REVIEW: THERMOREGULATION IN CHELONIANS

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### INTRODUCTION

Temperature is a major factor in the ecology and physiology of reptiles and since the early pioneering studies of Strelnikov (1934), Sergeev (1939) and Cowles and Bogert (1944) which demonstrated that reptiles do not passively respond to environmental heat distribution but have the ability to behaviourally regulate their body temperatures, there has been a wealth of information published on the subject. There have also been numerous reviews of these studies. One of the earliest (Brattstrom, 1965) described the body temperatures of approximately 160 species of reptiles. The most recent and extensive (Avery, 1982) discussed the thermal relations of over 500 species; however much of this information concerned lizards, and relatively few of the cited papers dealt with chelonians. Yet the thermal relations of chelonians are of interest for several reasons. The animals are often approximately hemispherical in shape which means a relatively small surface to volume geometry compared to other groups of reptiles with similar mass, and thus they experience slower overall rates of heating and cooling. Some species also grow to a very large size. This may provide them with some degree of inertial homeothermy but may also impose excessive heat loads through difficulties of finding adequate shade (Swingland and Frazier, 1979). The terrestrial forms move only very slowly (Jayes and Alexander, 1980; Williams, 1981) and this may also present difficulties from overheating even in small species which at certain times of the year have to restrict movement through areas with limited shade (Meek, 1984; Branch, 1984). The semi-aquatic forms invariably live in habitats with a wide range of thermal conditions. In the Spring and Autumn in temperate zones, a terrapin that has been basking on a log beside a pool and achieved a high body temperature may suddenly be exposed to very cool conditions when entering water. Therefore mechanisms for conserving body heat could have selective advantages for aquatic species (Bartholomew, 1982).

In this paper we review recent work on the thermal relations of chelonians — mainly those papers which have been published since the reviews by Hutchison (1979), Mrosovsky (1980: sea turtles only), Sturbaum (1982) and Avery (1982). There has been much progress in understanding chelonian thermoregulation in the past 10 years. This has been along three broad fronts:

- i. An increase in the number of species for which thermoregulatory data are available, together with the provision of more information relating to some of the well-studied species.
- ii. An increasing understanding of the mechanisms of behavioural thermoregulation, although as we shall show, progress in this area has been disappointingly slow.
- iii. An increased understanding of the physiological mechanisms which increase the efficiency of thermoregulatory processes, together with the physiological and other consequences of adaptations of this kind.

### BEHAVIOURAL THERMOREGULATION

Thermoregulatory behaviour in reptiles is a mechanism which has evolved to satisfy physiological thermal requirements by exploiting thermally diverse microenvironments in the habitat. In chelonians, thermoregulatory behaviour has been observed in all of the three major life forms: terrestrial, semi-aquatic and marine (Avery, 1982).

#### TERRESTRIAL CHELONIANS

The first descriptions of the thermal relations of chelonians were in terrestrial species which were shown to be diurnal heliotherms maintaining body temperatures above 30°C (Sergeev, 1939; Bogert and Cowles, 1947; Woodbury and Hardy, 1948; review in Avery, 1982). Recent studies have reinforced these findings. In North African *Testudo graeca*, early morning basking enables the animals to attain body temperatures up to 35°C (Lambert, 1981; Meek and Jayes, 1982) after which locomotor activity, feeding and mating take place. If the skies are overcast, however, there is prolonged basking through the middle of the day (Lambert, 1981), as there is in coastal areas which are subjected to sea mists (Meek and Jayes, 1982). Behavioural thermoregulation enables *T. graeca* in North Africa to maintain relatively high and relatively constant body temperatures for most of the daily period following initial basking (Lambert, 1981; Meek and Jayes, 1982).

This ability has been observed in other species. The South African *Chersina angulata* maintains body temperatures which are on average 4-6°C higher than air temperatures by movement in and out of sunlit and shaded areas (Branch, 1984). In scrubland areas in

## Terrestrial chelonians

<i>Chersina angulata</i>	Branch, 1984
* <i>Gopherus flavomarginatus</i>	Aguirre Leon <i>et al.</i> , 1980
<i>Testudo graeca</i>	Lambert, 1981 Meek and Jayes, 1982 Wright <i>et al.</i> , in press
<i>Testudo hermanni</i>	Meek and Inskoop, 1981 Meek, 1984, in press a, b Hailey <i>et al.</i> , 1984 Pulford <i>et al.</i> , 1984 Chelazzi and Calzolari, 1986 Wright <i>et al.</i> , in press

## Semi-aquatic chelonians

<i>Chelydra serpentina</i>	Obbard and Brooks, 1981
<i>Chrysemys picta</i>	Graham and Hutchison, 1979 (laboratory) Peterson, 1986 (hibernation)
<i>Clemmys guttata</i>	Graham and Hutchison, 1979 (laboratory) Ernst, 1982
* <i>Mauremys caspica</i>	Meek, 1983
* <i>Mauremys japonica</i>	Ishihara, 1979
* <i>Pelomedusa subrufa</i>	Miller, 1979
<i>Pseudemys scripta</i>	Crawshaw <i>et al.</i> , 1980 Crawford <i>et al.</i> , 1983 Jarling <i>et al.</i> , 1984 Spotila <i>et al.</i> , 1984
<i>Sternotherus odoratus</i>	Graham and Hutchison, 1979 (laboratory) Ernst, 1986b
<i>Terrapene carolina</i>	Erskine and Hutchison, 1981 (laboratory)
* <i>Trionyx sinensis</i>	Khosatsky, 1981

## Marine chelonians

<i>Caretta caretta</i>	Spotila and Standora, 1985
<i>Chelonia mydas</i>	Standora <i>et al.</i> , 1982 Spotila and Standora, 1985
<i>Dermochelys coriacea</i>	Standora <i>et al.</i> , 1984 Spotila and Standora, 1985

TABLE I: A list of species for which data on body temperature has been published between 1981 and 1987, together with references. The Table also lists references prior to 1981 which were inadvertently omitted from Avery's (1982) comprehensive review. Species for which data are recorded for the first time are indicated by an asterisk (\*). All studies were carried out in the field unless the citation is marked 'laboratory'.

Yugoslavia *T. hermanni* basks in Spring throughout the morning, elevating body temperatures to around 34°C (Meek and Inskoop, 1981; Meek, 1984) with feeding, mating and locomotor activity during the middle and later periods of the day. In hot weather individuals of this species avoid moving extensive distances onto open clearings to reduce the risk of overheating (Meek, 1984) and this has also been observed in *Chersina angulata* (Branch, 1984). In the Autumn when the weather is cooler, basking intensity in *T. hermanni* increases, and the body temperatures at which feeding and locomotor activity take place are lower (Meek, 1988). In France *T. hermanni* occurs in woodland habitat with limited areas of sunlight, and although it may attain high body temperatures it has not been observed basking and appears for a large part

of the day to operate as a thermoconformer. In the afternoon body temperatures may exceed air temperatures by 4°C but it is not certain if the animals do indeed bask or whether the difference is due to metabolic heat production (Pulford *et al.*, 1984; see below).

The patterns of activity in *T. hermanni* vary between regions and with season. In Yugoslavia during Spring and Autumn activity is unimodal (Meek, 1984, 1988) but in Summer, both in Yugoslavia and at a coastal heathland in Greece, basking and activity are bimodal (Hailey *et al.*, 1984; Meek, 1988). In woodland populations in southern France summer activity is unimodal perhaps reflecting the lower heat loads in this habitat (Pulford *et al.*, 1984). Nevertheless it is interesting that maximum body temperatures of 34-

35°C have been measured in all of the populations studied so far, except during cooler Autumn weather. In areas of Greece where *T. hermanni* and *T. graeca* are sympatric, body temperatures of *T. hermanni* are on average lower than those of *T. graeca*; this is a reflection of differences in habitat utilisation (Wright *et al.*, in press).

A recent paper has demonstrated an unexpected element of subtlety in the thermoregulatory relationships of *T. hermanni* with its environment. Chelazzi and Calzolari (1986) have shown that in Italian tortoises thermoregulatory efficiency is dependent on habitat familiarity. This was demonstrated by introducing tortoises into an area alongside resident animals and monitoring their temperature and behaviour. Resident tortoises were found to reach maximum body temperatures on average two hours each day earlier than introduced animals and their body temperatures were less dependent on environmental temperatures; introduced animals behaved as thermoconformers with body temperatures closely tracking air temperatures. It was suggested that this thermal lag could have important ecological consequences for non-residents by reducing daily activity time and in females by affecting the maturation of ova. Clearly it would be of interest to know the length of time involved for a tortoise to familiarise itself with a new habitat and become a proficient thermoregulator. Such information could be important in conservation projects, for example when reintroducing captive-reared tortoises into areas where populations have been depleted through collection or habitat deterioration.

The work of Chelazzi and Calzolari also illustrates a need for investigation of the *mechanisms* by which chelonians respond with appropriate behaviour patterns to the thermal environment. What cues do they use? Experiments have shown that the lizard *Lacerta vivipara* may use light intensity, direction and distribution as cues (Avery and D'Eath, 1986; D'Eath, 1987). It is not known whether chelonians determine the distribution of heat in the environment in similar ways. This is an important gap in knowledge. Many observations and experimental results could be more readily interpreted if this information was available, for example nest site selection in *Testudo hermanni* and *Emydoidea blandingii*, which is believed to be governed by choice of substrates and temperatures which will optimise environmental sex determination (Swingland and Stubbs, 1985) — but see Meek (in press) for an alternative view — or embryological development (Gutzke and Packard, 1987).

The importance of environmental temperatures for successful incubation as a factor which influences the distribution of species is emphasised in a study of *Testudo graeca* in Morocco by Lambert (1983). This study shows that rainfall is also a contributory factor. In our opinion this promising approach could be extended even further to include the constraints imposed by thermoregulatory behaviour on the remaining activity patterns of the animals.

The results described above may give the impression that thermoregulatory considerations are always a major determinant of behaviour patterns in terrestrial

chelonians. This is not always the case, however; water balances appear to be of primary importance in the desert tortoise *Gopherus agassizii* (Nagy and Medica, 1986).

#### SEMI-AQUATIC CHELONIANS

It can be seen that the terrestrial chelonians which have been studied conform to the classic paradigm of diurnal heliothermy which has been investigated most thoroughly in lizards (Avery, 1982; Huey, 1982). The thermoregulatory behaviour of semi-aquatic chelonians is more variable and less easy to understand. Avery (1982) has discussed the complexities of thermoregulatory behaviour in these animals, drawing attention to studies which suggest that whilst the primary function of basking is to increase body temperature, it may have other functions.

Recent work has supported the view that the primary function of basking is thermoregulatory. The African terrapin *Pelomedusa subrufa* does not bask on non-sunny days or in a laboratory thermal gradient if the heat lamps are not switched on, but on sunny days it shuttles on and off basking sites, elevating body temperatures to around 37°C. The body temperatures of dead *P. subrufa* on basking areas may reach 54°C (Miller, 1979), which far exceeds the critical maximum of any chelonian (Hutchison *et al.*, 1966) demonstrating that thermoregulation whilst basking must involve a balance between heat losses and heat gains. Relationships between the frequency of terrestrial basking and weather conditions have been shown in *Pseudemys scripta* (Spotila *et al.*, 1984), *Chrysemys picta* (Bury *et al.*, 1979; Schwarzkopf and Brooks, 1985), *Pelomedusa subrufa* (Miller, 1979) and *Chelydra serpentina* (Ewert, 1976). These relationships have been analysed from a partly theoretical standpoint by Crawford *et al.*, (1983).

Two species which operate over a particularly wide range of body temperatures (3-32°C and 7.5-30°C respectively), are *Clemmys guttata* and *C. insculpta*; to a certain extent they are thermoconformers (Ernst, 1982, 1986a). Basking nevertheless occurs in both species; it is more frequently observed in females in late May and early June (Ernst, 1986a). Many species show latitudinal or seasonal differences in thermoregulatory behaviour, e.g. *Pseudemys scripta*, although in this case Spotila *et al.* (1984) have shown that it is the timing of behaviour which changes with latitude; the responses of the animals to the same environmental stimuli are similar in different parts of the range. The differences in timing are clearly adaptive.

There has been much debate about the functions of basking in semi-aquatic chelonians. It has frequently been shown that the frequency or duration of basking increase after feeding (see reviews and discussion in Huey, 1982 and Avery, 1982), but this does not always occur — basking in *Chrysemys concinna* for example, did not increase significantly after feeding (Henneman, 1979).

The thermal strategies of terrapins are clearly opportunistic. This is well illustrated by the study of *Pseudemys scripta* (which is the most extensively-studied terrapin species) by Spotila *et al.*, (1984), which

demonstrates aquatic basking (raising body temperatures to 1-3°C above ambient water temperature) and selection of heated areas of water in the outflow from a nuclear reactor. Thermoregulation in *P. scripta* is further discussed in an environmental context by Spotila and Standora (1985b). Crawford *et al.* (1983) suggested that terrapins might be able to reduce the amount of time thermoregulating by selecting basking areas with high operative environmental temperatures (these are rather complex measures of the heat which is available in the environment) and would therefore shift basking sites as the day progressed.

Other factors which may influence thermoregulatory behaviour have also been examined, for example the substrates of basking areas may determine bask duration (Boyer, 1965). Concrete has a high thermal conductivity and this may explain why Meek (1983) observed only limited basking by *Mauremys caspica* at a concrete irrigation channel in North Africa, although those individuals which did bask attained body temperatures of around 29.5°C. *Pseudemys scripta* thermoregulate to a selected temperature range when in a thermal gradient (Crawford *et al.*, 1980) and Jarling *et al.* (1984) have shown that there is a diel rhythmicity underlying this temperature selection with differing thermoregulatory behaviour between morning and afternoon.

The work of Erskine and Hutchison (1981) demonstrates that the pineal hormone melatonin may play a role in setting the temperature around which terrapins, like other reptiles (Firth and Turner, 1982), may thermoregulate. This is likely to become an active area for research in the next few years.

Hibernating terrapins do not appear to thermoregulate, despite some earlier reports that they might do so (work on *Chrysemys picta* by Peterson, 1986). Peterson also provides an important discussion of the problems in defining 'environmental temperature' in situations where radiant heat sources are negligible or absent.

#### MARINE CHELONIANS

Most of the recent studies of marine turtle thermoregulation have concentrated on physiological aspects (see below); there has been no major advance in understanding behaviour since Avery (1982) wrote 'Marine turtles may also absorb solar radiation whilst floating at the surface. Considerable elevation of shell temperature, and rather smaller elevation of deep body temperature, was reported in *Chelonia mydas* floating in shallow sea water in captivity (McGinnis, 1968). Under these conditions, a radiotelemetered 42 kg *Caretta caretta* maintained differentials between body and sea of up to 3.75°C when the sun was shining; it failed to do so on an overcast day (Sapsford and van der Riet, 1979). Further work is clearly needed to determine the significance of solar radiation for these animals'.

#### PHYSIOLOGICAL ASPECTS OF THERMOREGULATION

Ever since the discovery that sea turtles might exhibit some degree of endothermy there has been

intense interest in their thermoregulatory physiology (reviews in Bartholomew, 1982; Spotila and Standora, 1985a). It is perhaps not surprising, therefore, that this is the aspect of chelonian thermoregulation which has received most attention during the past 10 years. Standora *et al.* (1982), in a careful study of the distribution of heat in *Chelonia mydas* using sonic transmitters, radiotransmitters and implanted thermistors, showed that body temperatures of inactive adult turtles were rarely more than 1-2°C above the temperature of the surrounding water. Vigorously-swimming turtles, on the other hand, had temperatures in the pectoral region raised by as much as 7-8°C. It was only in the actively-moving parts of the body that temperatures were raised, however; calculations showed that the metabolically-derived heat would be unable to warm the whole body faster than about 1°C h<sup>-1</sup>. Similar, although less detailed, experiments with *Dermochelys coriacea* gave essentially similar results (Standora *et al.*, 1984). Experiments on heat exchange rates suggest that larger turtles have a greater ability to thermoregulate than smaller specimens (Smith *et al.*, 1986).

Similar experiments on the heat exchange rates of terrapins have shown interesting differences between species. Soft-shelled turtles *Trionyx spinifer* heated faster than they cooled in water (by as much as a factor of two in small (<0.5kg) animals) but cooled faster than they heated in still air. Heart rates during heating exceeded heart rates during cooling at the same body temperatures in both media. This difference, called hysteresis, is particularly large in the marine turtle *Chelonia mydas* (Smith *et al.*, 1986). The ability of *Trionyx* to alter heat exchange rates is greater than that of any previously reported ectotherm in the same size range (Smith *et al.*, 1981; see also Khosatzky, 1981). *Terrapene ornata*, by contrast, showed no differences in thermal time constants (which are a measure of heat exchange rates) or heart rates when heated or cooled in water; their ability to adjust physiological control is clearly limited, and these animals must rely on behavioural mechanisms to thermoregulate (Adams and deCarvalho, 1984). How much this species actually does thermoregulate in nature is unclear, however (Fitch, 1956; Legler, 1960).

It is disappointing that physiological aspects of thermoregulation in terrestrial chelonians have not recently been studied, particularly in view of the relatively large size of some species and the insulating properties of the shell (Standora *et al.*, 1982). Spotila and Standora (1985) have shown how in a large *Chelonia mydas* walking on land along a beach in Costa Rica under the hot sun, deep body temperature rose by 7.8°C h<sup>-1</sup> (over 23 minutes), carapace surface temperature by 50.4°C h<sup>-1</sup> to reach 53.8°C, and plastron surface temperature by 16.7°C h<sup>-1</sup> to reach 42.9°C. They demonstrated that a nesting turtle would experience severe heat stress, even during overcast weather, and that if it attempted to nest during the day it would probably need to return to the water to prevent overheating before nesting was completed. Meek (in press) has reported on the rates of heat gain by a nesting *Testudo hermanni* under both hazy sunshine and when the sky was overcast. The data

suggest that during hot sunny weather nesting female tortoises too would run the risk of dangerously overheating, even at the latitude of 42° where this study was carried out.

The analysis of Spotila and Standora (1985) also demonstrates conditions which would enable sea turtles to bask on land (as they sometimes do, e.g. in the north western Hawaiian Islands, Whittow and Balazs, 1982), mainly when there is a sea breeze, relatively low levels of solar radiation, and using cooling strategies such as flipping sand onto their carapace and rear legs. These kinds of analyses could with profit be extended to terrestrial chelonians.

#### GENERAL CONSIDERATIONS: THE IMPORTANCE OF INTEGRATED STUDIES

It will have become apparent in this review that in those areas of chelonian thermoregulation where interest has been greatest — endothermy in marine turtles, the functions of basking, the ecological and behavioural constraints imposed by thermal limitations and requirements — a number of investigators have been active in publishing the results of experiments and observations. Progress in overall understanding has been slow, however. The reason for this has in our opinion been a lack of *integrative* studies in which physiological, ecological and behavioural factors have been investigated simultaneously, and considered as essential components in the complex of factors which has shaped natural selection in chelonians. Detailed studies, and especially those taking advantage of technological advances such as those in radioisotopes (e.g. Ward *et al.*, 1976), telemetry (e.g. Standora, 1982; Standora *et al.*, 1984) and infra-red thermography (e.g. Avery and D'Eath, 1986) must continue. Synthetic, integrative studies should however now be given a higher priority for further research.

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## HYPOTHESIS:

### A GEOLOGICAL BASIS FOR SOME HERPETOFAUNAL DISJUNCTIONS IN THE SOUTHWEST PACIFIC, WITH SPECIAL REFERENCE TO VANUATU

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## INTRODUCTION

Vanuatu is generally considered to form part of the Outer Melanesian Arc, which runs from New Guinea through the Solomons and eventually to Fiji and Tonga (Holloway, 1979). Within the arc, however, Vanuatu is relatively isolated by the surrounding Johnson Trough, Vitiav Trench and Vanuatu Trench (Coleman, 1970). A spreading ridge is present to the east of the group. Recent work (Chase, 1971) indicates that until 6-8 mybp Vanuatu lay north of Fiji and Tonga, along the border of a wider arc, adjacent to the Vitiav Arc (Carney and MacFarlane, 1982). Until the Miocene Vanuatu maintained its position relative to Fiji. At that time it began to drift. Subsequent arc bending and counterclockwise rotation has resulted in its present position (Gibbons, 1985). This theory is consistent with the current thought that many orogenic belts are actually composites of smaller blocks (terrane) of varied origins (Craw, 1982). In general, support for the terrane accretion origin of

composite regions comes from magnetic anomalies, heat flow studies, bathymetry and stratigraphy. Terranes of the North American Cordillera (Irving, 1979; Coney *et al.*, 1980) and the central Philippines (McCabe *et al.*, 1982, 1985) have been particularly well documented. Terranes of the former have been used in an attempt to explain the biogeography of bolitoglossine salamanders (Hendrickson, 1986) and it is possible that some of the peculiarities of animal distribution in Vanuatu may also be explained by its past fragmentation and movement.

## THE VANUATUAN FAUNA AND ITS AFFINITIES

The herpetofauna of Vanuatu has traditionally been regarded as depauperate Paupuan (Baker, 1928, 1929; Darlington, 1948), having suffered attrition through filter effects that have reduced diversity away from the New Guinea source area. This 'impoverished' fauna has, however, been supplemented by species of

presumed New Caledonian origin (*Leiolopisma atropunctatum*) as well as by endemics, chiefly associated with a localised radiation of the scincid genus *Emoia* (Medway and Marshall, 1975). Although this evaluation of the Vanuatuan reptile fauna can explain the origin of most native species, it is limited in that it accounts for the taxa present by invoking equilibrium theory (McArthur and Wilson, 1963, 1967), an approach more nearly appropriate for biogeographical problem over ecological time than for those over geological time. Recent advances in the geology and paleogeography of the southwest Pacific (e.g. Chase, 1971) suggest explanations for the distribution of certain 'problem' groups of amphibians and reptiles in Pacific biogeography (e.g. *Platymantis* and *Perochirus*) while maintaining the applicability of existing hypothesis for the origin of more recently arrived and vagile groups. Gibbons (1985) first suggested the application of knowledge of the changing paleoposition of Vanuatu to herpetological problems. This paper expands on his views and suggests that initial reference to historical biogeographical implications for distribution may provide fruitful results in the analysis of the faunal origins and relations of older island groups.

Like that of other Outer Arc elements, the fauna of Vanuatu shows Papuan affinities with limited local endemism. Mega- and microchiroptera are the only native mammals, and fully half of the land birds are shared with New Guinea (Medway and Marshall, 1975). Further, the number of bird species in Vanuatu is in accord with the predictions of the McArthur-Wilson model. The herpetofauna is particularly poor in comparison with neighbouring New Caledonia or even with Fiji, further to the east. The Earl of Cranbrook (Medway and Marshall, 1975; Cranbrook and Pickering, 1981; Cranbrook, 1985) recognised a Vanuatuan terrestrial reptilian fauna of 20 species. In addition, there is one introduced species of hylid frog, *Litoria aurea* (Meday and Marshall, 1975; Fischthal and Kunzt, 1967; Tyler, 1979). To this list may be added several additional endemic *Emoia* (W. C. Brown, in press) and perhaps *Crocodylus porosus*, identified from the trackways on Espiritu Santo (Baker, 1928, 1929). Further, *Gehyra vorax*, now generally recognised as specifically distinct from *G. oceanica* (contra Burt and Burt, 1932), has also been recorded from Vanuatu (Baker, 1928, 1929; Boulenger, 1885). The Fijian iguana, *Brachylophus fasciatus* has been introduced to the fauna recently by man (pers. comm., W. C. Brown). Of Vanuatuan reptiles *Gekko vittatus* (not included by Medway and Marshall, 1975) and *Gehyra mutilata* are known from single specimens collected by Baker (1928, 1929) and probably do not constitute native species. Similarly, the snake *Ramphotyphlops braminus* is likewise a recent addition, probably transported by man (Meday and Marshall, 1975). I accept the remaining taxa (approximately 21 species) as constituting the native herpetofauna of Vanuatu.

A distinct break between the faunas of New Caledonia and Vanuatu, especially in regard to the herpetofauna of these areas, was noted by Roux (1913), Baker (1928) and Sternfield (1920). Sub-

sequently, differences in the snail fauna (Solem, 1958) have also been indicated. In all cases the richer fauna occurs in New Caledonia and shows distinct affinities with New Zealand and especially Australia, in contrast to the poorer, Papuan fauna of Vanuatu. Cheesman (1957) noted breaks within the flora of Vanuatu and suggested that the southern islands, Aneityum, Erromanga and Tanna had probably been connected with New Caledonia during the Cretaceous, when both split off from Queensland. She believed that subsequent division occurred in the Late Miocene or Early Pliocene. Solem (1958) presented conflicting evidence from land snail distributions and pointed out the existence of the 6400m Vanuatu Trench separating the two regions. Among animal groups, only highly vagile forms and some parasitic groups such as the Diptera pupipara (Maa and Marshall, 1981) show a strong affinity across the Vanuatu Trench. Current views of plate tectonics clearly indicate that Vanuatu and New Caledonia have never been in contact and generally account for the differences in the faunal, and to some extent, floral affinities of the two areas.

As noted by Roux (1913) and Gibbons (1985), the Loyalty Islands, located approximately 100km off the east coast of New Caledonia and 150km from the southern islands of Vanuatu, possess an intermediate herpetofauna best characterised as a depauperate New Caledonian fauna with some typical Papuan elements and very low endemism. Brown (1956) considered the Loyaltys as the link between New Caledonia and the rest of Southern Melanesia. Berlioz (1962) also noted the Vanuatuan influence in the Loyaltys' avifauna. The age of the emergent Loyalty Islands is unknown, but appears to be very recent, perhaps Pleistocene. Thus the herpetofauna is probably only of recent origin, being derived via overwater dispersal, although parts of Maré may have been emergent for a much longer time and may, at one time, have been much closer to the New Caledonian source area.

The relationship of Vanuatu to other elements of the Outer Melanesian Arc, notably the Solomon Islands and Fiji, is more problematic. As mentioned, the herpetofauna of Vanuatu is slightly poorer than that of Fiji, which is more distant from the Papuan source area (elements of the Outer Arc have never been broadly connected by land, thus overwater dispersal is likely to have been responsible for the introduction of the fauna of the eastern elements of the arc). The Fijian herpetofauna, as reviewed by Pernetta and Watling (1979) consisted of 22 species of reptile and three amphibians (excluding the semi-marine *Crocodylus porosus*, Derrick, 1965). The addition of newly described species of *Emoia* (Brown and Gibbons, 1986), *Brachylophus* (Gibbons, 1981) and *Leiolopisma* (Zug, 1985), as well as the inclusion of *Ramphotyphlops flaviventer* and the removal of introduced forms (*Bufo marinus*, *Hemidactylus frenatus*, *H. garnotii* and *Hemiphyllodactylus typus*) yields a native fauna of about 27 species, including the two ranid frogs, *Platymantis vitianus* and *P. vitiensis*. The existence of the iguanine, *Brachylophus*, present in Fiji, Tonga and Wallis Island, is generally explained by overwater dispersal from the Americas (Cogger, 1974; Gibbons, 1981, 1985). If this is the case, its absence in Vanuatu

(where it has subsequently been introduced) would not be surprising.

The absence in Vanuatu of frogs of the genus *Platymantis*, however, is perplexing. These ranids are speciose in the Solomon Islands and are represented by two endemic species in Fiji. Schmidt (1930) hypothesised differential extinction in Vanuatu in order to reconcile this gap with a continental, or Papuan, origin of the genus. If Brown's (1952) assertion that the ranids are an old group in the Solomons (and Fiji) is correct, the appearance of Vanuatu at its present position in the Neogene would seem to explain the absence of Vanuatuan *Platymantis*. However, Tyler (1972) considered the ranids as having Pleistocene entry into the Solomons, and thus into Fiji. It seems difficult to reconcile the latter view of platymantine origins with the terrane theory of Vanuatuan origin. The most recent discussion of the age of this group (Zweifel and Tyler, 1982) implies that the platymantines have inhabited the region since the Miocene.

As first suggested by Gibbons (1985) the presence of elapids (*Ogmodon*) in Fiji but not in Vanuatu is likewise accounted for by the relatively recent shift of Vanuatu into a southern position. The distributions of *Ramphotyphlops flaviventer* in Fiji and the Solomon Islands superficially suggests a similar explanation, but upon closer examination this seems unlikely given the difficulty in locating typhlopids, their ability to be transported in soil and the uncertain status of even alpha level systematics in *Ramphotyphlops*. The absence of Vanuatu would also have left Fiji closer to a New Zealand/New Caledonian source area for *Leiolopisma* and account for the absence of unique species of this genus in Vanuatu.

Another anomaly of the Vanuatuan fauna is the presence of *Perochirus guentheri*. This gekkonine is known from few specimens (Medway and Marshall, 1975; Brown, 1976) and its congeners occur only on Guam, Tinian, Ponape, Marcus Island, the Truk Islands and Kapingamarangi Atoll, all in Micronesia. While speculative, a former, northern position of Vanuatu might account for the presence of this species (Gibbons, 1986), as a position to the north of Fiji would have 'exposed' Vanuatu to dispersing migrants from the northwest. Prior to this suggestion the only existing hypothesis for the disjunct distribution of *Perochirus* had been the past existence of a continental mass connecting virtually all of the islands in the Pacific (Baur, 1897).

For the remainder of the herpetofauna of Vanuatu, a more traditional explanation (i.e. dispersal along a track from New Guinea through the Solomons) of origin seems on the basis of species diversity to apply. Thus, for both *Emoia* and the boïd genus *Candoia* species diversity is highest in the Solomon Islands and drops to the south and east. Although speciation has occurred in Vanuatu and elsewhere among *Emoia* populations, morphological differences are minor and are not inconsistent with recent expansion in the Pacific. The remainder of the Vanuatuan species are broadly distributed in the western Pacific (*Gehyra vorax*) or are pan-Pacific — (*Cryptoblepharus boutonii*,

*Lepidodactylus lugubris*, *Gehyra oceanica*, *Lipinia noctua*, *Nactus pelagicus*), implying recent dispersal across their present ranges. Finally, there are those species with broad distribution which have been transported by aboriginal or modern man.

#### PATTERNS OF COLONISATION

The herpetofauna of Vanuatu exhibits a historical complexity that belies its modest diversity. At least four broad categories of colonisation by reptiles and amphibians have characterised the western Pacific. The first, and most complex of these, involves movement of taxa most parsimoniously explained by known changes in paleogeography of emergent land masses. Most of the western Pacific islands of Miocene or greater age obtained their faunas through prior contact with other land masses or through dispersal from adjacent regions (some now quite distant). The herpetofaunas of New Zealand and New Caledonia consist primarily of taxa ultimately derived from continental Gondwanaland (Bauer, 1986). In the case of Vanuatu, some faunal elements (e.g. *Perochirus*) may date from previously existing near-neighbour relationships with other island groups while other groups (*Platymantis*, elapid snakes) may have been excluded for the same reasons. This type of faunal origin, historical in the sense that there are geological clues to prior positions, allows for the prediction of distributed attributes of other animal and plant groups of suitable age.

A second category of colonisation by organisms is that based upon a probabalistic theory of dispersal with the framework of a static (or in other words, recent) geography. Predictions of the equilibrium models of island biogeography fit this mode and may be related to the distribution of *Candoia* and *Emoia* in Vanuatu.

Thirdly, wide ranging forms, which because of biological features such as reproductive characteristics (parthenogenesis, low egg-shell permeability, etc.) (Gibbons, 1985) may become distributed and established rapidly, without speciation (either because of maintenance of genetic contact or insufficient time or habitat differences). Examples in Vanuatu include *Lepidodactylus lugubris*, *Nactus pelagicus* and *Emoia cyanura*.

Finally, human assisted transport, either intentional or accidental, places a fourth level of complexity on distribution. The presence of species such as *Litoria aurea* and *Ramphotyphlops braminus* are known examples of this category of colonisation. Although the last two modes are primarily responsible for the distribution of reptiles in the eastern Pacific (Ineich, 1982; McKeown, 1978), Vanuatu, and the western Pacific are influenced by all four.

The view of Vanuatu as a recent entrant into the Outer Melanesian Arc seems the most reasonable explanation of apparent herpetofaunal anomalies of the region, both on geological and zoological grounds. In addition to the herpetofaunal examples cited above, it also appears to explain disjunctions in the

distribution of a wide variety of groups in the Outer Arc (e.g. the Cryptotympanini [Insecta: Cicadoidea] Duffels, 1986). The analysis of faunal and floral elements in light of this information may yield further evidence of Micronesian, or simply northern, affinities in the Vanuatuan fauna, particularly in groups of pre-Neogene origin or arrival in the western Pacific.

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## POPULATION ECOLOGY AND CONSERVATION OF TORTOISES: THE ESTIMATION OF DENSITY, AND DYNAMICS OF A SMALL POPULATION

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### ABSTRACT

Part 1: Line transect methods were used in three areas with known densities of *Testudo hermanni*. This enabled calculation of the proportion of the population available for finding (PAF); that is, excluding tortoises in refuges or in thick cover. At times of peak daily activity PAF varied between about 0.1 and 0.3, and was greater in spring than in summer. Males had higher PAF than females on summer evenings, the main courtship period, and PAF of males was greater in a population with a male-biased sex ratio. Transect sampling is useful for estimating the density of tortoise populations, provided that the low PAF is taken into account. Values of effective transect width are given for a variety of habitat types.

Part 2: A small population of *T. graeca* at Alyki was studied between 1980-1986; its size was estimated at about 25 adults, with an even sex ratio. Immature animals were recruited into the adult population, which was stable or increasing during this period. Adult size and juvenile growth rate were similar to other coastal populations of *T. graeca* in the region. The implications for the conservation of endangered tortoises are discussed.

### INTRODUCTION

The threat to Mediterranean tortoise populations from collection for the pet trade (Lambert, 1969, 1979, 1981a) has now ended. The problem of habitat loss is, however, still present (Lambert, 1984; Cheylan, 1984).

Basic information on tortoise populations is needed to evaluate this threat (Honegger, 1981; Groombridge, 1982). This paper considers two aspects of the population ecology of tortoises which have special relevance to conservation.

## PART 1: ESTIMATING THE POPULATION DENSITY OF TORTOISES

### INTRODUCTION

At present there is no tested method for the rapid estimation of the population density of Mediterranean tortoises. Short term mark-recapture studies may give misleading results. For example after a short study, Stubbs, Espin and Mather (1979) calculated that there were about 400 *Testudo hermanni* in an area of heathland; a later estimate from several man-months of study in the same area was over 3,000 tortoises (pre-fire estimate of Stubbs, Swingland, Hailey and Pulford, 1985). Sighting frequency gives a relative measure of abundance, if weather, time of day and season are taken into account (Lambert, 1981b), but does not give an absolute value for population density. It is sensitive to minor features of the habitat, such as the noisiness of leaf litter (Hailey, Pulford and Stubbs, 1984) and type of tortoise activity (Lambert, 1981b), and so may produce misleading comparisons between sites.

Line transect methods enable population density to be calculated from sighting frequency (Burnham, Anderson and Laake, 1980). They depend, however, on the animals being available for sighting, and tortoises are known to be inactive for much of the time (Auffenberg and Iverson, 1979). The first part of this paper calibrates the effect of low activity, by applying line transect methods to three areas where population density of *T. hermanni* is known from long-term mark-recapture studies.

### METHODS

All line transect methods are of the form

$$D = N / 2.L.W. \quad (1)$$

where D is population density, N animals are seen along a transect of length L, and W is a measure of one half of the effective width of the strip sampled (Seber, 1981). This relation may be expressed in terms of sighting frequency (F) by replacing N/L by F/S, where S is walking speed. Low activity is taken account of by including a term for the proportion of the population which is available for finding at the time of sampling (PAF), so that

$$D = F / 2.S.W.PAF \quad (2)$$

Tortoises in refuges (usually shallow scrapes under vegetation, termed pallets), or stationary in dense cover, are seldom seen during transect sampling (see Hailey *et al.*, 1984), and are therefore considered to be unavailable for finding.

Two methods of calculating the effective width are used here; these differ in the way in which the curve of numbers found against distance from the transect (the sighting profile) is described:

(a) If the sighting profile shows exponential decrease, that is a concave shape, then

$$W = \bar{x}$$

where  $\bar{x}$  is the mean distance of sightings perpendicular to the transect (Caughley, 1977).

(b) Using the flexible power curve method of Eberhardt (1968),

$$W = 2.\bar{x}.k(k+2) / (k+1)^2$$

where k describes the shape of the sighting profile, and is estimated by regression (Caughley, 1977). Concave, linear, and convex sighting profiles give k less than 1, exactly 1, and greater than 1, respectively.

These methods were used in three areas where population density was known from long-term mark-recapture studies: the Massif des Maures, France (Stubbs and Swingland, 1985), and two separate populations at Alyki, Greece (Stubbs *et al.*, 1985). Sampling was by slow walking along irregular transects, passing around shrubs and areas of dense cover. Initially this was done throughout the day, to identify the periods of peak activity, but was then restricted to peak periods to measure maximum sighting frequency. This work was carried out in August 1981 and April 1982 (France) and in July-August 1982 and April-May 1983 (Greece). Time spent handling tortoises was excluded from calculations of sighting frequency. The distance of each sighting perpendicular to the transect was paced out, and the paces were calibrated against a 30m line for each observer. Sighting profiles were also constructed from data collected during mark-recapture studies throughout 1981-1983.

There were three main vegetation types at Alyki. Coastal heath: open loose sand and dunes, with a sparse cover of herbs. Dry heath: firm sandy soil with scattered shrubs, herbs and grasses. *Juncus* marsh: rushes, asphodels and dense grass, in damp areas. Most work was done in two separate areas of dry heath; a 55 ha part of the main heath, and the 7 ha salt works heath. These areas and vegetation types are described in more detail by Stubbs, Hailey, Tyler and Pulford (1981) and Stubbs *et al.*, (1985). The habitat of the Massif des Maures was mostly dense evergreen oak forest, with some maquis at higher altitudes. Apart from a few cultivated clearings used by adults during the May-June nesting season (Swingland and Stubbs, 1985), the forest was a closed canopy with dense undergrowth and a thick noisy leaf litter.

It was not possible to measure the distance of sightings perpendicular to the transect in the forest. Searching was modified to a walk-stop-listen pattern, as the noise of walking interfered with finding tortoises, most of which were located by sound. This type of sampling has been described by Emlen (1971). As there was no real transect, distances of sightings perpendicular to it (PD) could not be found. However, the straight distance (SD) between the observer and each tortoise was measured. The two distance measures are related by

$$PD = SD.\text{Sin } \Theta$$

where  $\Theta$  is the angle between the sight line and the transect. If angles around the observer are random, as when animals are detected by sound, then on average

$$PD = SD.0.64$$

(0.64 is the mean Sin  $\Theta$  for all angles between 0 and 180°). Sighting profiles in forest were therefore constructed using 0.64.SD. This adjustment is

Vegetation type	x (m)	k	W (m)	N	% by sound
Evergreen forest	5.1	1.28	8.2	2110	84
Maquis	4.9	2.32	8.9	105	81
<i>Juncus</i> marsh	3.0	0.47	3.2	234	35
Dry heath	4.2	0.96	6.2	610	18
Coastal heath	6.7	1.06	10.2	123	12

TABLE 1: Descriptive statistics of sighting profiles of *T. hermanni* according to vegetation type. All tortoises larger than 10cm straight carapace length, except those in pallets. The sample size (N) and the percentage of the sample detected by sound are also shown.

unsuitable for more open areas where most animals are found by sight, where the mean sighting angle is usually about 33° (Burnham *et al.*, 1981).

RESULTS

EFFECTIVE WIDTH

Sighting profiles for juveniles (less than 10cm straight carapace length) were narrower than those of larger tortoises (Fig. 1). Juveniles were therefore excluded from further analysis; tortoises longer than 10cm are subadults or adults. There were only slight

differences between sighting profiles for spring and summer, or between males and females (Fig. 2). The data for different seasons and for the sexes were therefore pooled.

Sighting profiles differed between the vegetation types (Fig. 1). The effective width of the strip sampled was greatest in evergreen forest and maquis, where tortoises could be heard over long distances, and in coastal heath, where they could be seen easily (Table 1). Effective widths calculated by method (b) were greater than mean distances from the transect (method a). This difference was greatest in evergreen forest and maquis, where sighting profiles were convex, with k greater than 1. Sighting profiles were approximately linear in dry heath and coastal heath, with k about 1. Only in *Juncus* marsh was the exponential model a good fit.

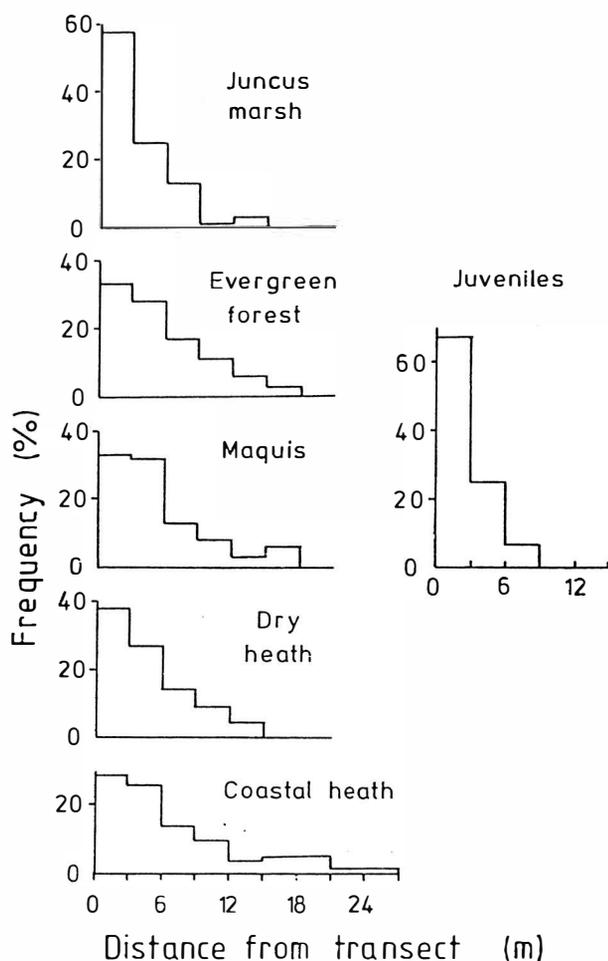


Fig. 1 Sighting profiles of adult and subadult *T. hermanni* in different vegetation types, and of juveniles (n = 110) in dry heath. Sample sizes and descriptive statistics for the vegetation types are given in Table 1.

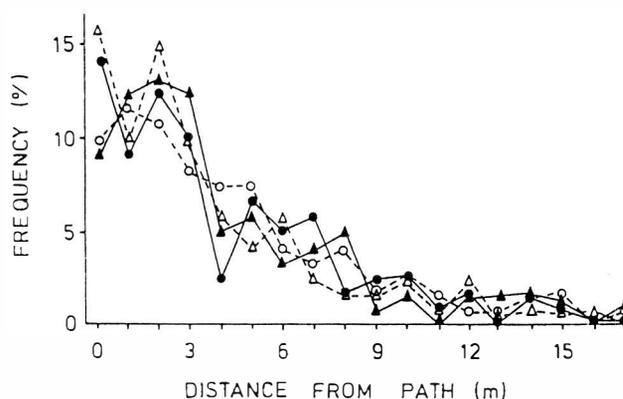


Fig. 2 Sighting profiles of *T. hermanni* in evergreen forest in the Massif des Maures: variation with sex and season. ●-females, summer; ▲-females, spring; ○-males, summer; △-males, spring.

SIGHTING FREQUENCY AND PAF

There were morning and evening peaks of sighting frequency in both areas of dry heath in Greece, in both spring and summer; the peaks were closer together and there was some midday activity in spring. The mean sighting frequency during the peak periods is shown in Table 2. Walking speed was 3km.h<sup>-1</sup> on the main heath, and 2.5km.h<sup>-1</sup> on the smaller salt works heath. In France, activity was at a uniform level between 10-17h local time in late summer (late August and early September), with a mean sighting frequency of 2.6 males.h<sup>-1</sup> and 1.3 females.h<sup>-1</sup>. In spring, peak sighting frequency was found between 12-15h; 4.3 males.h<sup>-1</sup> and 3.6 females.h<sup>-1</sup>. Walking speed was 2.0km.h<sup>-1</sup>.

	Main Heath		Salt Works Heath	
	Males	Females	Males	Females
Spring 08-12h	13	4.6	7.2	7.6
17-19h	24	9.9	—	—
Summer 08-11h	9.2	2.3	5.6	4.1
18-21h	17	2.3	11	5.4

TABLE 2: Sighting frequency (No.h<sup>-1</sup>) of *T. hermanni* in two populations at Alyki: means for peak activity periods (local times shown) in spring 1983 and summer 1982. All tortoises larger than 10cm SCL, except those in pallets. There was no data for the salt works heath during spring afternoons.

Population density of subadult and adult *T. hermanni* in the 55ha of the main heath covered by sighting frequency observations, and in the salt works heath, were estimated from Stubbs *et al.* (1985) as:

Main heath 18 males 8.4 females ha<sup>-1</sup>  
Salt works heath 20 males 19 females ha<sup>-1</sup>

The average density of adults and subadults over the 35ha Massif des Maures study area was about 10ha<sup>-1</sup> (Stubbs and Swingland, 1985). Sighting frequency observations were made in the most intensively studied 9ha of the study area, where all resident tortoises had been marked; they also exclude the nesting season (when non-residents migrate into this area). The density of resident adults and subadults was therefore used; 5.2 males and 4.4 females ha<sup>-1</sup>.

The proportion of the population which was available for finding at the time of peak activity is shown in Table 3. This was calculated from equation (2), using the effective width for evergreen forest and dry heath (Table 1), and the values for walking speed, population density and peak sighting frequency above. It is striking that even during peak periods, only a minority of the population was available for finding. Even the highest sighting frequency recorded, 30 males and 8 females h<sup>-1</sup> (early evening in spring on the main heath) corresponds to availability of only 49% of males and 27% of females.

## DISCUSSION

### PROPORTION AVAILABLE FOR FINDING

Bury and Luckenbach (1977) and Morgan and Bourn (1981) have indicated that census methods (that

is, grids or transects) are better than mark-recapture for estimating the population density of tortoises. These studies used animals which can be found even when inactive; *Gopherus* in burrows in the desert, and giant tortoises under the scarce shade trees, respectively. This paper shows how transect methods can be extended for use on the small Mediterranean tortoises in scrub habitats.

General discussions of line transect sampling assume that all animals in an area are available for finding, that is PAF = 1.0 (Caughley, 1978; Seber, 1981). Using this value would result in a five or ten fold underestimate of population density of *T. hermanni*. The effect of non-availability has probably been neglected because transect methods were developed for birds and large mammals, which are rarely inactive during peak activity periods. Reptiles, however, spend only a small part of their time active (Huey, 1982).

Line transect methods are a suitable method for rapid estimation of tortoise population density if this low activity is taken into account. The values of PAF in Table 3 may be used as a rough adjustment for future surveys. I suggest general values for PAF of:

Summer; 0.15 for males and 0.1 for females  
Spring; 0.25 for both sexes.

Effective width *W* is best calculated from sighting profiles using method (b) above, although the values in Table 1 could be used for areas of these habitats with very low density where sample sizes were low.

In the only previous correction for activity on survey methods for Mediterranean tortoises, Lambert (1981b) suggested that about 60% of animals in an area would

Population sex ratio	Main Heath		Salt Works Heath		Massif des Maures	
	Males	Females	Males	Females	Males	Females
	2.1:1		1.0:1		1.2:1	
Spring AM	0.19	0.15	0.12	0.13	—	—
Midday	—	—	—	—	0.25	0.25
PM	0.36	0.32	—	—	—	—
Summer AM	0.14	0.074	0.090	0.070	—	—
Midday	—	—	—	—	0.15	0.090
PM	0.25	0.074	0.18	0.092	—	—

TABLE 3: The proportion of *T. hermanni* available for finding (PAF) at peak activity periods in three populations of known density. Calculated from equation (2) in the text. All tortoises larger than 10cm SCL; the population sex ratios from mark-recapture studies are also shown.

be found by normal, non-intensive searching during the optimum activity period. I obtain a different result from his data, as follows. On average, a captive female *T. graeca* spent 12% of the daily active period actually moving. Two thirds of field sightings were moving, so that the total sample was 1.5 times the number of moving animals. By analogy with the captive female, the moving animals would be 12% of these present in the area sampled. Therefore only 18% of the tortoises in an area would be found, similar to values of PAF reported here.

DIFFERENCES BETWEEN SEXES

Availability for finding of males and of females was similar in spring, in all three populations. This is a period when there is little courtship (at least in these populations; Swingland and Stubbs, 1985), most activity being basking and feeding. Males were, however, more available for finding than females in summer, especially in the evening which is the main time of courtship (Hailey *et al.*, 1984). Both sexes were more available for finding in spring than in summer, in all three populations.

The relationship between tortoise activity and availability for finding will be considered in detail elsewhere. The low availability for finding in summer is known to be due to low activity, from a study using thread-trailing (Hailey, in preparation). Summer activity is probably limited by the increased time needed to process dry food (Coe, Bourn and Swingland, 1979). Mediterranean tortoises are apparently completely inactive in summer in very dry areas (Raxworthy, Rice, Smith and Claudius, 1984).

In summer, PAF of females was similar in the three populations. However, males were more available for finding on the main heath, where the population sex ratio was biased with more than two males per female (Stubbs *et al.*, 1985). The best comparison is with the saltworks heath, which had similar habitat, adult population density, and PAF of females to the main heath; the only differences were the population sex ratio and the PAF of males. The simplest hypothesis is that males were more active on the main heath because of greater competition for females: this will be examined elsewhere.

PART 2: DYNAMICS OF A SMALL POPULATION

INTRODUCTION

Five of the 39 living species of tortoise are now endangered (Anonymous, 1986). One species, *Geochelone yniphora*, is one of the 12 most threatened animals in the world (Hoogmoed, 1985), with a total population in the wild and in captivity of only 100-400 individuals (Curl, Scoones, Guy and Rakotoarisoa, 1985). In addition to the causes of their present status, small populations have the problems of locating mates and of inbreeding; they are also difficult to study. The ecology of any small natural population of tortoises is therefore of interest as a model for the chronically endangered species. This section concerns a very small

population of *T. graeca* at Alyki, information about which has been collected over seven years during study of a large population of *T. hermanni*.

METHODS

The same methods, and a common markingscheme, were used for both species (Stubbs *et al.*, 1984, 1985). Sampling was carried out in summer 1980 and 1982 and in spring 1983, and between April 1984 and November 1986. Sector 9 was examined most frequently in 1986 to obtain more information on the population on *T. graeca*. The size at sexual maturity in *T. graeca* from northern Greece is not known precisely. In this paper, males of 14cm and females of 16cm straight carapace length are considered to be adults.

RESULTS

DISTRIBUTION AT ALYKI

*Testudo graeca* at Alyki were largely restricted to the coastal heath in sectors 8 and 9 (Fig. 3a), in contrast to *T. hermanni* which was found all over the site (Stubbs *et al.*, 1985). Within the coastal heath area, *T. graeca* was more common in the central, exposed part, while *T. hermanni* was more often found in peripheral areas with greater plant cover (Fig. 3b). The role of habitat use in niche separation of *T. graeca* and *T. hermanni*, and its consequences, are discussed by Wright, Steer and Hailey (MS). These authors also consider the distribution of *T. graeca* in Greece, and the possible origins of the Alyki population.

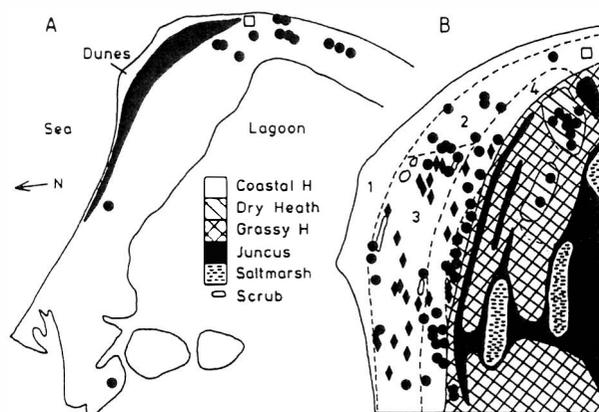


Fig. 3 (a) Distribution of *T. graeca* over the Alyki heath. The shaded area shows the main area occupied by this species, ● show all sightings of individuals outside this area between 1980-1986. The lighthouse (□) marks the border between the main heath and the southern heath to the south. (b) An enlarged map of sectors 8, 9 and 12, showing details of vegetation and sightings of individual *T. graeca* (◆) and *T. hermanni* (●) in July-October 1986. Within the coastal heath, both species avoided the dunes (1); *T. hermanni* was prevalent in peripheral areas with *Artemisia* (2) or herbs (4), and *T. graeca* was prevalent in the central exposed part (3). *T. hermanni* was also found in sector 12, especially the areas of dry heath.

There was a possibility that the few *T. graeca* found on the main heath represented the edge of a larger population centred in the southern heath. A survey in

the summer of 1985 (Wright, Steer and Hailey, MS) therefore concentrated in the southern heath. In total, 365 individual tortoises were handled on the southern heath between 1980-1986: only eight of these were *T. graeca*. The southern heath *T. graeca* were all small, length range 58-122mm. This is the size at which the related *T. hermanni* are thought to disperse, the adults holding stable home ranges (Stubbs and Swingland, 1985). It is therefore assumed that the *T. graeca* in sectors 8 and 9 were the main population, with a few dispersing juveniles reaching the southern heath.

POPULATION SIZE

The population of adult *T. graeca* was estimated from analysis of recaptures to be at most 14 males and 12 females (Table 4). In total, 15 adult males and 11 adult females were handled, most of them in several years (Fig. 4); 13 males and 9 females were known to be alive in 1986. The population therefore comprised about 25 adults, with an approximately even sex ratio.

	1980	1982	1983	1984	1985	1986
(a) Jolly-Seber estimates of adult population size.						
Males	—	8	7	14*	9	—
Females	—	6	6	11*	12*	—
(b) Numbers of new immature tortoises marked each year, and number of these recruited to adults by 1986.						
Marked	5	3	3	4	10	7
Recruited	4	2	1	0	0	—

TABLE 4: Size of and recruitment to the adult population of *T. graeca* at Alyki, in the years 1980-1986. \* rounded up, otherwise integer results.

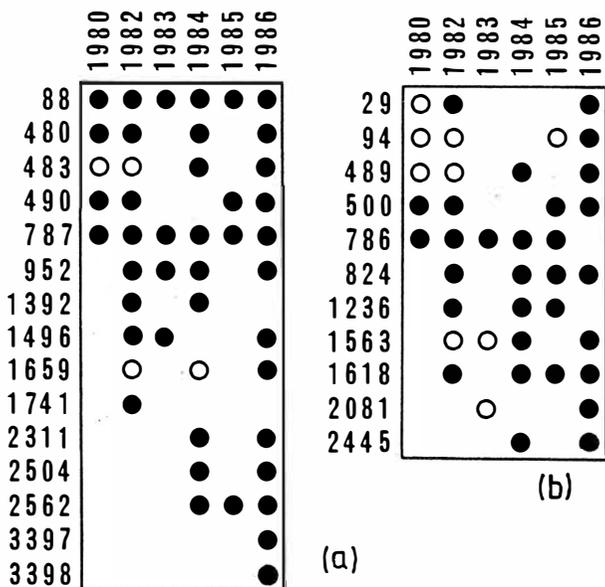


Fig. 4 Captures of individual adult *T. graeca* at Alyki in different years; (a) males (b) females. Tortoises were numbered using the scheme of Stubbs *et al.* (1984). Some tortoises were immature when first captured and were recruited into the adult population; capture when immature is shown as 0.

POPULATION DYNAMICS

Minimum survival rates of adults can be calculated from the data in Fig. 4. Eight males were handled in 1982, of which at least six were alive in 1986, equivalent to annual survival of 0.93 (= 0.75<sup>1/4</sup>). The

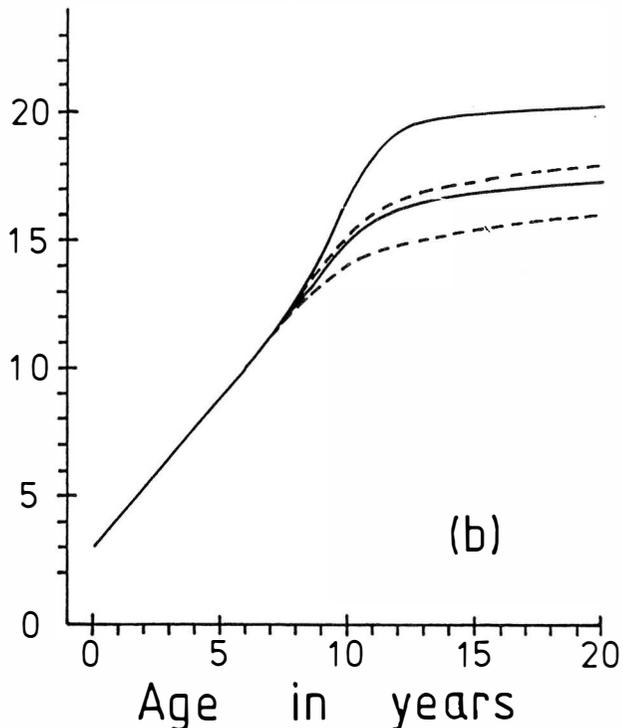
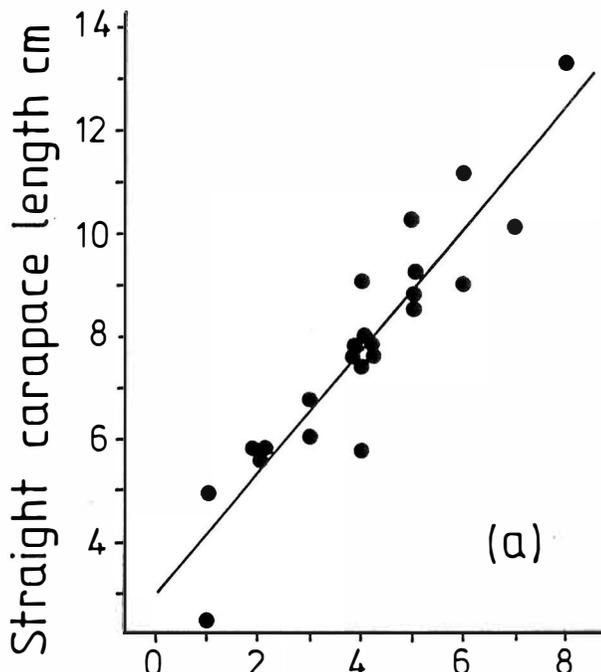


Fig. 5 (a) Relation between number of growth rings and body size of *T. graeca* at Alyki; all tortoises with 8 or fewer rings, including recaptures in different years. The regression line from Table 5 is also shown. (b) Growth curves for *T. graeca* (—) and *T. hermanni* (---) at Alyki, from the curves of growth rate on length in Fig. 6. The two curves for each species are for females (above) and males. Growth of juveniles is the average of the growth ring — length regressions in Table 5.

Site	Species	a	b	SEb	N	SCL <sub>6</sub>
Alyki	<i>T.h.*</i>	38	10.9	1.14	50	103
	<i>T.h.</i>	37	10.0	2.37	38	97
	<i>T.g.**</i>	30	11.8	1.07	23	101
Epanomi	<i>T.h.</i>	21	12.9	2.61	21	98
	<i>T.g.</i>	32	11.3	0.95	99	100
Keramoti	<i>T.h.</i>	26	11.5	2.75	11	95
	<i>T.g.</i>	32	10.9	1.76	35	97

TABLE 5: Statistics of the regressions of straight carapace length (SCL, in mm) on number of growth rings. All tortoises with eight or less rings, including recaptures. a is the SCL at age 0 and b is the growth rate in mm.year<sup>-1</sup>, with standard error. SCL<sub>6</sub> is the estimated length at age six. Data are from animals handled during summer 1985, except: \* random sample of those handled in 1984; \*\* all those handled 1980-1986.

corresponding figures for females are; six handled 1982, four recaptured 1986, giving minimum annual survival of 0.90.

Thirty-two immature *T. graeca* were handled in total. Some of these were recruited into the adult population during the study. Of the 11 immature *T. graeca* first marked before 1984, seven were recaptured and of adult size by 1986 (Table 4b).

GROWTH

Growth rings in scutes are unreliable indicators of age in adult tortoises (Castanet and Cheylan, 1979; Stubbs *et al.*, 1985), and so only those of tortoises with eight or less rings were considered. These are compared to data for *T. hermanni* at Alyki, and for *T. graeca* and *T. hermanni* examined by Wright *et al.* (MS) at several sites in summer 1985. There was a linear relationship between straight carapace length and growth ring number in all the populations studied; data for *T. graeca* at Alyki are shown in Fig. 5a. Regression parameters for these populations are shown in Table 5. These all predict hatchling length of about 30mm, and growth to about 10cm after six years. The 95% confidence limits of all slopes overlap the mean of 11mm.year<sup>-1</sup>.

Observed growth of *T. graeca* between captures in alternate years is shown in Fig. 6. The pattern of growth in tortoises, and the relation between observed growth and growth rings, will be considered in detail elsewhere. It is of interest here to compare growth of *T. graeca* and *T. hermanni* at Alyki, as both of these have been measured over two years. Data for *T. hermanni* were for exactly two years, from summer 1980 to summer 1982, and are from Fig. 6 of Stubbs *et al.* (1985).

Growth rates at 10cm were similar in the two species. In males, the curve for *T. graeca* was shifted to the right, so that they grew at the same rate but maintained growth at larger sizes. In females, *T. graeca* grew faster as well as for longer. The average curves of growth rate on length are converted to curves of size on age in Fig. 5b: growth between hatching and 6 years is from the average of the growth ring equations from Table 5. Fig. 5b emphasises that male *T. hermanni* stop growing before male *T. graeca* and female *T. hermanni*, and that female *T. graeca* grow at an even faster rate.

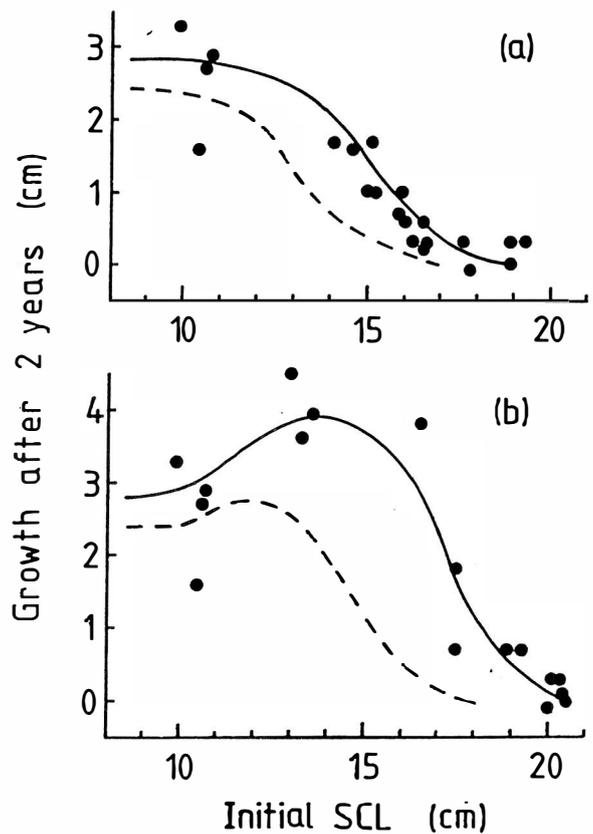


Fig. 6 Growth in length after two years against initial length of *T. graeca* at Alyki, with curve fitted by eye (—); (a) males, (b) females. Juveniles are included in both parts. Curves for growth of *T. hermanni* after two years (---) were fitted by eye to the data in Fig. 6 of Stubbs *et al.* (1985).

DISCUSSION

The population of *T. graeca* at Alyki consisted of about 25 adults, occupying an area of 15 ha. Despite this small size and low density, the population showed no decline over a seven year period; indeed Table 4 shows an increasing trend. The vigour of the population can also be considered at the level of individual tortoises. Adult *T. graeca* were of similar size to, or larger than, those at other sites in northern Greece (Wright *et al.*, MS); they were not stunted. Juveniles grew at similar rates to those at other sites

(Table 5). Small populations of tortoises may therefore be ecologically viable.

The question of genetic viability in the long term is more difficult to judge; the average loss of variation due to inbreeding can be calculated, but not the effect of this on ecological vigour. Theoretically, a population of 25 animals would lose half of its present degree of heterozygosity in about 33 generations (Fig. 33.2 of Strickberger, 1976); over 500 years for Mediterranean tortoises (generation time is longer than the age at sexual maturity). The problem of inbreeding should therefore not cause immediate concern in tortoise conservation. For example, it may be better to protect several small populations in situ, rather than pool them in a single reserve, with the possible problems of relocation (Berry, 1986).

A small population of animals sympatric with a large population of a closely related species has an additional problem. Individuals of the rare species will encounter the common species much more frequently than they will encounter conspecifics. This may result in the breakdown of reproductive isolation (Tinsley, 1981). The reproductive potential of the rare species would then be lowered by infertile eggs or hybrids. Courtship of *T. graeca* at Alyki has only been observed seven times, and one of these was with a female *T. hermanni*. Hybridisation in *Testudo* has been observed in captivity (review in Kirsche, 1984); the impact on wild populations awaits further study, although tortoises with apparent hybrid characteristics have been found in the wild (Sofianidou, personal communication, and personal observations).

#### ACKNOWLEDGEMENTS

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## OBSERVATIONS ON GUT FUNCTION IN *MAUREMYS CASPICA CASPICA* (GMELIN)

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### ABSTRACT

Adult *Mauremys c. caspica* consume relatively small quantities of food (average 0.06% body wt day<sup>-1</sup>; food in dry state). The large females eat more than the small males both absolutely and relatively. The oesophagus acts as a food storage organ for as much as 3-4 hours. The gut clearance time is of the order of 72 hours, but transport of food along the gut is considerably slowed by food deprivation. The absorption efficiency of *Mauremys c. caspica* during routine feeding was 46.4%.

### INTRODUCTION

Observations on gut function in aquatic chelonians have so far been relatively sparse, although sea turtles have attracted some attention in recent years (Bjorndal, 1980; Hadjichristophorou and Grove, 1983; Davenport and Oxford, 1984; Birse and Davenport, 1987), particularly the green turtle *Chelonia mydas* L. which is herbivorous as an adult.

*Mauremys c. caspica* is a predominantly carnivorous, freshwater emydid turtle which features pronounced sexual dimorphism, at least in the Saudi Arabian population (age-for-age, females weigh about 5-6 times as much as males). The study reported here was designed to investigate appetite, gut transit time and absorption efficiency in adult *Mauremys*, with a view to comparing these parameters with those of sea turtles and other chelonians.

### MATERIALS AND METHODS

#### COLLECTION AND MAINTENANCE

The specimens used in this study were collected in the late 1970s in Saudi Arabia. They have since formed a breeding colony at the University College of North Wales, but only seven adult males (mean weight 130g; range 101-173g) and four females (mean weight 815g; range 762-866g) were used in the investigation reported here. The turtles were held in enclosures (2 metres x 1 metre; half land; half water) supplied with running fresh water and kept at 25 ± 1°C. Routine feeding was *ad lib* with trout pellets (Omega: floating) which have previously been used in studies upon juvenile *Chelonia mydas* and *Caretta caretta*. Some of the female turtles laid eggs within a month of the end of the study.

#### APPETITE

Five turtles (2 male, 3 female) were individually fed every 24 hours for 5 days. In the case of each meal for each animal a quantity of dry trout pellets were weighed and the turtle fed 1 pellet at a time until it had

refused 5 pellets in 10 minutes. Offered, but uneaten pellets were dried in an oven then weighed with the unoffered pellets to allow the determination of the amount of food consumed (as g dry weight).

#### GUT TRANSIT TIME

Two approaches were adopted to assess gut transit time. Firstly, two turtles (both male) were X-rayed and then fed a satiation meal of trout pellets labelled with barium sulphate (2% w/w; thoroughly mixed in by grinding together with pestle and mortar). The animals were X-rayed again at the following intervals after the meal: 1, 2, 3, 5, 8, 12, 15, 18, 24, 30, 36, 48, 54 and 72 hours. During this period the animals were fed daily on trout pellets, which they swallowed whole.

Secondly, two groups of turtles (A and B, each of 5 turtles) were each fed satiation meals of trout pellets labelled with chromic oxide (which is green in colour, non-toxic and not absorbed across the gut). As with barium sulphate, the chromium oxide was thoroughly mixed with the material of the pellets. Group A was subsequently fed daily upon normal trout pellets for 6 days. Group B was starved for 10 days. Each turtle was held in a separate aquarium fitted with a slatted floor which prevented breakup of faeces. The colour and quantity of faeces produced by each animal was recorded daily.

#### ABSORPTION EFFICIENCY

To estimate absorption efficiency, several turtles were fed a chromic oxide-labelled meal for several days until green faeces had been produced for at least 2 days. Samples of food and faeces were then collected and analysed for energy content by bomb calorimetry. Chromic oxide content was analysed spectrophotometrically.

### RESULTS

Estimates of feeding rate are shown in Table 1. From this table it can be seen that feeding rate varies considerably from day to day in both sexes. On average

Turtle Wt (g)	Sex	Mean daily Satiation Ration (mg dry wt)	Satiation ration as % body weight per day					Mean daily Satiation Ration (% body weight)
			Day					
			1	2	3	4	5	
866	F	730	0.136	0.003	0.085	0.071	0.127	0.084
856	F	600	0.087	0.007	0.046	0.086	0.124	0.070
120	M	43	0.080	0.000	0.050	0.010	0.040	0.036
136	M	39	0.035	0.009	0.053	0.018	0.027	0.028
121	M	84	0.120	0.040	0.060	0.129	0.080	0.070

TABLE 1: Estimation of daily satiation meal size.

the turtles consumed food equivalent to about 0.06% body weight day<sup>-1</sup>. Against expectation, the much larger females not only consumed far more food than males in absolute terms, but also ate rather more (mean 0.077% body weight day<sup>-1</sup>) on a weight specific basis than males (mean 0.045% body weight day<sup>-1</sup>).

## GUT TRANSIT

X-radiographs illustrating the progress of a barium meal through the gut of a male turtle (154g) are shown in Fig. 1. Portions of the gut were identified by dissection of preserved specimens of *Mauremys* of similar size. Five minutes after a meal, *all* food was

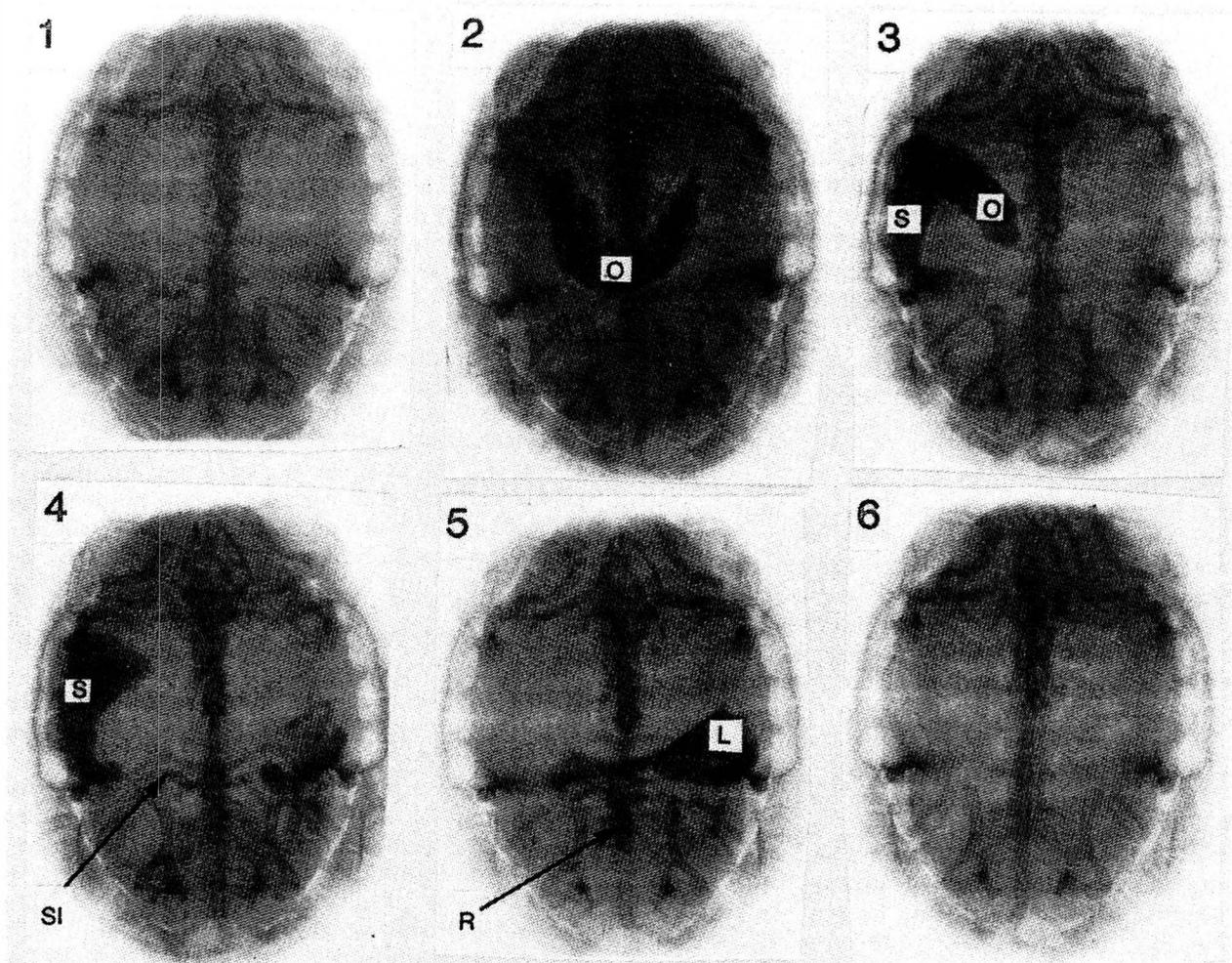


Fig. 1 X-radiographs to show passage of food through the gut of *Mauremys c. caspica*. Fig. 1 Turtle immediately before feeding. Note that the head is retracted within the shell. Fig. 2 5 minutes after ingestion of barium meal. The whole meal is within the oesophagus. Fig. 3 2 hours after the meal. Some food has moved to the stomach, but a considerable quantity remains in the oesophagus. Fig. 4 12 hours after the meal. Food may be seen in stomach, small intestine and large intestine. Fig. 5 36 hours after the meal. All material has now accumulated in large intestine; faeces can be seen in rectum. Fig. 6 72 hours after meal. No barium shadow remains.

Key: O = oesophagus, S = stomach, SI = small intestine, L = large intestine, R = rectum.

Group	Turtle No.	Sex	Days after labelled meal										
			1	2	3	4	5	6	7	8	9	10	
A	1	F	—	—	—	G	G	B*					
	2	F	—	G	G	—	G	B					
	5	M	—	G	G	B/G	B	B					
	6	M	—	—	(G)	B	B	—					
	7	M	—	—	B/G	B	B	B					
B	3	F	—	—	B/G	—	G	(G)	G	G	—	G	
	4	F	—	—	—	—	—	—	(G)	—	—	—	
	8	M	—	—	—	—	B	(G)	—	(G)	—	—	
	9	M	—	—	—	G	B/G	G	(G)	—	—	—	
	10	M	—	—	G	G	G	(G)	—	(G)	(G)	—	

Key: B = brown, G = green, B/g = brown and green, s \* copious faeces, ( ) = sparse faeces.

Table 2: Faecal colour in turtles fed a chromic oxide-labelled meal on Day 0.

found in the lower part of the oesophagus, which evidently acts as a food storage organ, since considerable quantities of food still remained in it when two hours had elapsed after the meal. Only after 3-4 hours had all food moved onwards into the stomach. Small quantities of food had entered the small intestine after 3 hours and some had reached the large intestine by the time 12 hours had elapsed. Progressively the stomach emptied, no barium shadow being visible after 36 hours. The gut was completely clear of barium after 72 hours. Similar results were obtained with another turtle of slightly smaller size (121g).

Table 2 shows the results derived from the feeding of chromic oxide-labelled meals. Animals in group A which, which were fed normal meals after their chromic oxide meal produced green faeces between 2 and 5 days after the meal. Brown (i.e. chromic oxide-free) faeces appeared 4-5 days after the meal and all animals produced brown faeces on day 6. Group B animals, which were starved after the chromic oxide meal showed a very different pattern of faecal production. No green faeces were produced until 3 days had elapsed; small quantities of green faeces were still being produced after 9-10 days. Clearly, starvation slows and inhibits transport of material along the gut.

#### ABSORPTION EFFICIENCY

The energy content of dried faeces was measured for five individuals (one on two separate occasions) and 2 or 3 determinations were made on each sample (the number depending upon the amount of available material). The mean faecal energy content was 12.6KJg<sup>-1</sup> (SD = 1.0). The energy content of dry trout pellets (2 determinations) was 17.8KJg<sup>-1</sup>. The chromic oxide content of faeces was 9.5µmg dry weight<sup>-1</sup> (n = 5; SD = 1.5); that of food was 7.2µmg dry weight<sup>-1</sup>.

The mean absorption efficiency (calories) was therefore:

$$\left(1 - \frac{7.2/17.8}{9.5/12.6}\right) \times 100\% = 46.4\%$$

#### DISCUSSION

The daily dry mass ration eaten by specimens of *Mauremys* (0.06% body weight day<sup>-1</sup>) is considerably smaller than that recorded for young green and loggerhead sea turtles of similar size (*Chelonia mydas*, 2-3% body weight day<sup>-1</sup> according to Hadjichristophorou and Grove (1983) and Davenport and Oxford (1984); *Caretta caretta*, <3.7% body weight day<sup>-1</sup> (Birse and Davenport, In Press)) and of young painted turtles (*Chrysemys picta*) which ate 0.125-0.5% body weight day<sup>-1</sup> according to Kepenis and McManus (1974). Obviously the energy requirements of rapidly growing juvenile animals are likely to be much greater than those of adult animals approaching their maximum size (though giant Aldabra tortoises of 25kg body weight eat 0.87% body weight day<sup>-1</sup> according to Coe *et al.* (1979)), but the feeding rates of *Mauremys* are remarkably low, presumably reflecting the species' low level of activity. Food intake can also be considered on an energetic basis. *Mauremys* takes in about 0.01KJg body weight<sup>-1</sup> day<sup>-1</sup> and absorbs some 0.005KJg body weight<sup>-1</sup> day<sup>-1</sup>. Corresponding mean values for *Chrysemys* (11-55g body weight) at 25°C were 0.10KJg body weight<sup>-1</sup> day<sup>-1</sup> and 0.08KJg body weight<sup>-1</sup> day<sup>-1</sup> (calculated from data of Kepenis and McManus, 1974), again indicating that *Mauremys* is a low activity, low energy demand emydid.

Despite a relatively low average feeding rate, specimens of *Mauremys* eat occasional large meals and appear to be adapted to take in large quantities of food quickly, since the oesophagus functions as a food store, holding food for more than two hours. Oesophageal food storage appears to be a not unusual feature of chelonians since we have now detected it in *Caretta caretta* (Birse and Davenport, 1987) and *Chelonia mydas* (Davenport *et al.*, In Press) as well. It may be suggested that oesophageal food holding was initially associated with head retraction in response to predator threat (swallowing is presumably difficult when the neck is contorted), with a storage function evolving later and persisting even in those

chelonian groups which have subsequently abandoned head retraction.

The difference in absolute feeding rates between male and female *Mauremys* is considerable (females ate 12 times as much as males), and graphically illustrates the energetic cost of maintaining an animal of sufficient size to lay clutches of large eggs. Sexual size dimorphism is quite common in emydid turtles and *Mauremys* from Saudi Arabia appear to be an extreme example of this phenomenon, which may not be invariable throughout the species' range since Pritchard (1979), in his general description of the species, states that males achieve the same maximum length as females, while Meek (1987) has recently reported that females of the closely related *Mauremys c. leprosa* are rather larger than males, particularly in late adulthood.

A total gut clearance time (T.G.T.) in *Mauremys* of 72 hours was indicated by both barium and chromic oxide meal studies. This T.G.T. is much shorter than those reported for sea turtles of similar size, which range from 122 hours in *Caretta caretta* (Birse and Davenport, 1987) to 176 hours in *Chelonia mydas* (Hadjichristophorou and Grove, 1983), and of giant tortoises (*Geochelone gigantea* in which it is about 240 hours (Hamilton and Coe, 1982). However, it is similar to the values reported for other emydids (*Pseudemys scripta*, 61 hours; *Chrysemys picta*, 59 hours) by Parmenter (1981). The relatively short gut transit time may help to explain the low mean absorption efficiency (energy) recorded of around 50%, although assimilation efficiencies of around 80% have been reported for *Chrysemys* which has even faster gut transit (Kepenid and McManus, 1974). For comparison, assimilation efficiencies of about 35% have been reported for herbivorous giant tortoises, while recent experiments (Davenport *et al.*, In Press) indicate that the absorption efficiency of omnivorous *Chelonia mydas* juveniles lies between 65 and 90%, being lower on a diet of sea grass than when the animals were fed fish.

The observation that food deprivation slows/inhibits movement of food along the gut in *Mauremys* is to be expected. The reasons for such slowing are likely to be complex. To a large extent such slowing may be adaptive, allowing prolongation of digestion to extract as much energy as possible from the food in the gut (see

Sibley (1981) for review), but there may also be a mechanical component in that the absence of later meals prevents effective peristaltic propulsion of material along the gut. In this slowing of gut transit *Mauremys* is similar to the sea turtles.

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## EFFECT OF ALTERED pH ON EMBRYOS AND TADPOLES OF THE FROG *MICROHYLA ORNATA*

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### ABSTRACT

Short term effects of altered pH on embryos and tadpoles of the frog *Microhyla ornata* were studied under laboratory conditions. Alterations in pH were made by using dilute hydrochloric acid and sodium hydroxide solutions.

Late gastrula stage embryos tolerated pH between 4 to 10.5, showing normal development and hatching. At pH 3 and below development was immediately arrested and the embryos were killed within a few hours. Between pH 3.2 and 3.6 there was gradual decrease in toxicity, however, development was often arrested at about tail-bud stage. At pH 3.8 there was only 20% mortality while survivors showed normal development.

In alkaline range, the maximum pH tolerated without any apparent ill effect on development and hatching was about 10.5. At pH 11.0 and above there was drastic effect on the embryos which caused immediate cell to cell disaggregation of the embryos within an intact vitelline membrane.

The effects of altered pH, especially acidic pH, were similar to those observed earlier with sodium chloride treatment. In either cases normal swelling of the embryonic perivitelline space was prevented.

There was no significant difference in the tolerance of the tadpoles to altered pH as compared to that of the embryos, however hind-limb stage tadpoles appeared to be slightly resistant to acidic pH and slightly more sensitive to alkaline pH.

### INTRODUCTION

Acid rains and acidic effluents are polluting aquatic bodies all over the world. Acidification of lakes and other waterbodies has been reported by several workers (Almer *et al.*, 1974; Wright *et al.*, 1976; Johnson, 1979). Effects of lake acidification on aquatic biota, especially fish, have been well documented (Beamish and Harvey, 1972; Lievestad and Muniz, 1976). Mortality of amphibian species due to acidification of habitats has also been observed (Pough, 1976; Pough and Wilson, 1977; Beebe and Griffin, 1977). Studies on toxicity of acidic bog waters and acidic mine drainages indicated that amphibians are sensitive to low pH (Porter and Hakanson, 1976; Saber and Dunson, 1978). In recent years laboratory studies have also been carried out to understand effects of low pH on amphibian development (Gosner and Black, 1957; Freda and Dunson, 1985 a,b; Clark and Hall, 1985; Beebe, 1986). There are, however, no data on any of the native amphibians regarding their tolerance to altered pH conditions. Since industrial activity generates acidic effluents and acid rains are not unlikely in the areas of high industrial activity, we have investigated short term effects of altered pH on different developmental stages of the frog *Microhyla ornata*.

### MATERIALS AND METHODS

Naturally fertilised eggs or tadpoles of the frog *M. ornata* were collected from unpolluted ponds around Pune. Embryos were manually dejellied and transferred to aged tap water until required. Solutions

of different pHs were made by mixing dilute hydrochloric acid and sodium hydroxide in aged tap water. The pH was adjusted accurately using a pH meter. Gross pH range was prepared with a difference of 0.5 units. Based on earlier experiments a fine range of pHs was prepared with a difference of 0.2 units between the subsequent pHs to determine lethal and critical pH for the embryos. Embryos and other developmental stages were exposed to these solutions in 200ml or larger glass bowls. Usually 10 embryos were exposed per 100ml of solution but for larger tadpoles 200-400ml solution was taken for a batch of 10 tadpoles. Aged tap water with a pH of about 7.6 to 7.8 and total hardness as well as total alkalinity below 50 ppm (as calcium carbonate) was used as a control medium during the experiments. The temperature of the water varied between 22 to 26° Celsius. The embryos and tadpoles were observed periodically under stereozoom dissecting microscope. At least 30 embryos or tadpoles were exposed to each of the pH tested. The experiments were carried out for 96 hours. Tests of such short duration are routinely carried out to determine toxic effects of pollutants on fishes and other animals. Further, hatching takes place in about 48 hours in this frog and hence 96 hours of treatment gives idea about the effects on embryonic development, hatching as well as effects on freshly hatched tadpole. At least 80% solution from each experimental bowl was replaced by fresh solution of identical pH every 24 hours to keep the pH variation minimum. Mortality and other effects were noted after every 24 hours and the data was used to calculate LC50 as per the Reed-Muench method (Woolf, 1968). Measurements were taken using stage and ocular micrometer.

RESULTS

The embryos kept as controls showed normal development and differentiation of head, trunk and tail region. At the end of first 24 hours, the embryonic perivitelline space (PVS) was considerably swollen. The embryos hatched as tadpoles at about 48 hours. At 96 hours all control tadpoles showed well developed head, eyes and tail region. Typical pigmentation also appeared on the dorsal side of the head. All such tadpoles were actively swimming by 96 hours.

In the gross acidic range (between pH 2.5 to 7.0) the embryos tolerated pH 4.0 and above without any apparent ill effect. At and below pH 3.0 there was immediate arrest of development and total mortality within few hours. Exposure of embryos to a fine range of pH between 3.0 to 4.0 showed that pH about 3.6 was critical pH. Upto pH 3.6 there was 100% mortality within 96 hours. Mortality was reduced at pH 3.8 and the embryonic development was also normal. Mortality data along with LC 50 values is given in Table 1A. Similarly, in alkaline range the embryos tolerated pH 10.5 and lower. However, at and above pH 10.8 the embryonic development was immediately arrested and there was immediate cell to cell disaggregation of the embryo. Exposure of the embryos to a fine range of alkaline pH between 10.0 to 11.0 indicated that critical alkaline pH was about 10.6 (see Table 1B). However, it may be pointed out that NaOH solutions were not very stable and did not maintain exact pH.

Measurement of diameter of the vitelline membrane (VM) was carried out at the beginning and at the end of first 24 hours of the experiment. The diameter of the VM in control embryos increased from about 1.4mm to about 4.3mm in 24 hours. (Figs. 1 and 2). The embryonic PVS thus increased considerably from late gastrula stage to late tail-bud stage under control conditions. In the embryos exposed to acidic pHs, the swelling of the PVS was significantly affected between pH 3.0 to 4.0. In the solution of pH 3.0 the embryonic

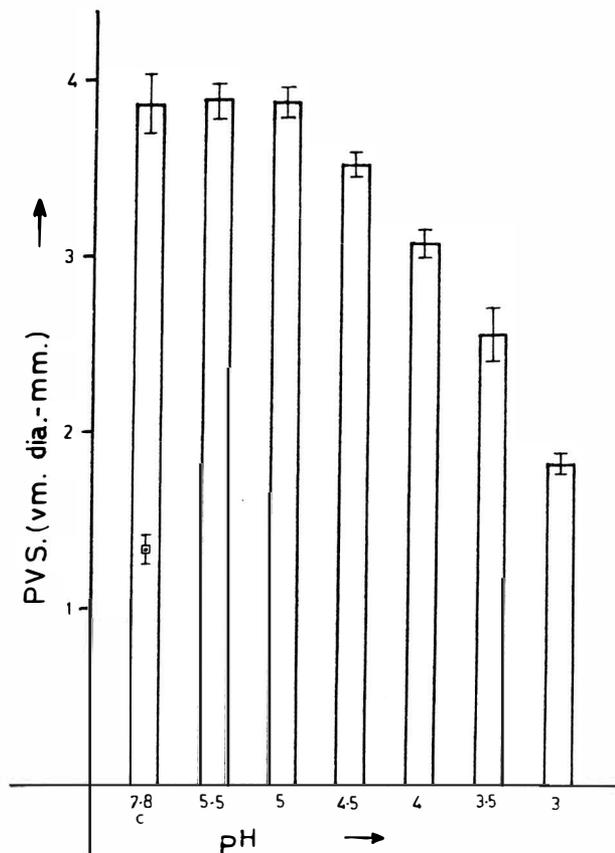


Fig. 1 Diameter of the perivitelline space of the embryos of *Microhyala ornata* after 24 hours of exposure of acidic pH. The mark inside the control (c) bars shows the diameter at the beginning of the experiment. Values listed are mean  $\pm$  S.D.

PVS remained almost unaltered (see Fig. 1). Similarly, in the embryos exposed to alkaline pH, there was adverse effect on swelling of the PVS (see Fig. 2). Though the PVS was also reduced at pHs between 4.0 to 5.0 and 9.5 to 10.5, the reduction was not severe. Further the embryos developed normally and were able to stretch the VM making room for the

(A)

Hours of Exposure	3.0	3.2	3.4	pH 3.6	3.8	4.0	'C' 7.8	LC50	95% Confidence limits
24	0	0	24	30	30	30	30	3.27	3.20-3.35
48	0	0	0	21	30	30	30	3.45	3.35-3.55
72	0	0	0	5	24	30	30	3.69	3.61-3.78
96	0	0	0	0	24	30	30	3.67	3.60-3.75

(B)

Hours of Exposure	'C' 7.8	10.0	10.2	pH 10.4	10.6	10.8	11.0	LC50	95% Confidence limits
24	30	30	30	30	18	0	0	10.66	10.32-11.02
48	30	30	30	30	18	0	0	10.66	10.32-11.02
72	30	30	30	30	18	0	0	10.66	10.32-11.02
96	30	30	30	30	9	0	0	10.54	10.48-10.60

TABLE 1: Tables showing survival of embryos exposed to different pHs prepared using HCl (A) and NaOH (B). Number of embryos exposed at each pH was 30. Hours of exposure were counted from late gastrula stage onwards. 'C' indicates control.

development. This resulted in curling of only the tip of the tail, a deformity which was not observed after hatching. However, at pH 3.8 the development was normal but the PVS was considerably reduced and, due to lack of enough space, embryos developed with curled body axis. Such embryos were swimming abnormally after hatching. Hatching of the embryos was not prevented at any pH between 3.8 to 10.5, although slight delay in hatching was observed upto pH 5.0.

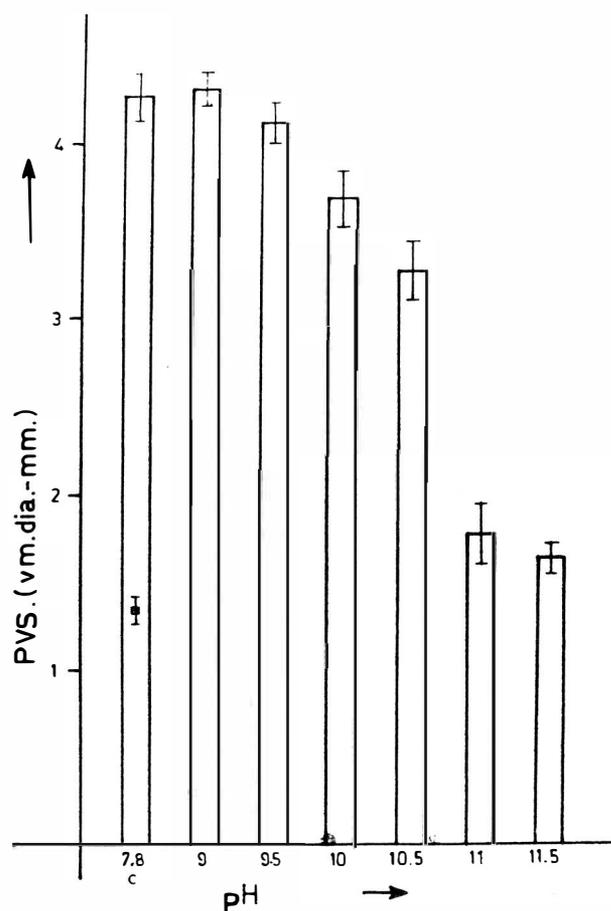


Fig. 2 Diameter of the perivitelline space of the embryos of *Microhyla ornata* after 24 hours of exposure to alkaline pH. The mark inside the control (c) bar shows the diameter at the beginning of the experiment. Values listed are mean  $\pm$  S.D.

Under similar treatment conditions, 10 day old tadpoles did not show any significant difference in the tolerance to altered pH as compared to that of the embryos. Hind-limb stage and older tadpoles however tolerated pH 3.5 which was lethal for the embryos. At the same time, hind-limb stage tadpoles were killed at pH 10.5, a pH well tolerated by the embryos. Thus the hind-limb stage and older tadpoles were slightly more tolerant of acidic and more sensitive to alkaline pH as compared to the embryos.

Erratic swimming, just after the release of the tadpoles into the media, was observed at and below pH 3.5 and at and above pH 10.5. At pH 11 disintegration of the tail fin was observed prior to death of the tadpoles. Effects at pH 11.5 were very severe and the tadpoles were killed within 3 to 5 minutes. Thus the lethal acidic pH for older tadpoles was 3.0 while the lethal alkaline pH was less than 10.5.

## DISCUSSION

Gosner and Black (1957) defined lethal pH as the one which causes irreversible cessation of normal development. According to this definition, the lethal acidic pH for *Microhyla* was 3.0 and the lethal alkaline pH was 11.0. None of the embryos exposed to the lethal pHs could survive and continue development. Gosner and Black also defined critical pH range and minimum limiting pH. The critical pH range solutions cause high mortality; and in our experiments this range was 3.2 to 3.6 for acid and 10.8 to 11.0 for alkali used. Minimum limiting pH is said to be the pH that allows normal development of more than 50% of the exposed embryos. In our experiments minimum limiting acidic pH was 3.8 because 80% of the exposed embryos survived and showed normal development at this pH. Limiting alkaline pH was found to be about 10.5. These values are comparable with those reported for other amphibians by Gosner and Black (1957), as far as acidic pH is concerned. There are no comparable data regarding alkaline pH. In case of acidic pH, older tadpoles were found to be more tolerant than embryos. Similar observations have been reported by Beebe (1986), who found that in the case of the natterjack toad, embryos and early tadpoles were killed around pH 4.0 while older tadpoles survived even at pH 3.5.

Our observation regarding prevention of swelling of the PVS of the embryos exposed to low pH is consistent with the reports published on other amphibians (Gosner and Black, 1957; Salthe, 1965; Freda and Dunson, 1985a). Reduction of PVS also occurs with salt treatment (Salthe, 1965; Gosner and Black, 1957; Padhye and Ghate, 1986). It is known that slow flow of water into PVS is necessary for normal development in amphibians (Krogh, 1939). Reduction in PVS observed in our experiments is probably related to change in osmotic gradients across the egg membrane, the gradient that is stated to decide the size of the PVS (Holtfreter, 1943). However, in our experiments, reduction in PVS was not severe to cause any deformity in the embryos exposed to pH between 4.0 to 10.5. Also, there was no significant effect on the hatching process, though severe curling of body axis and reduction in hatching success has been reported in case of other amphibians (Gosner and Black, 1957; Pough and Wilson, 1977; Freda and Dunson, 1985a; Clark and Hall, 1985). It is interesting to note that Dunson and Connell (1982) found that the curling and other deformities do not occur, and embryos survive the exposure to low pH, if the VM is removed, indicating that the chief cause of mortality associated with curling defect is membrane dysfunction. There being no direct effect on the embryo. They further hypothesised that low pH inhibited activity of hatching enzyme and (or) other mechanisms responsible for the enlargement of the PVS. Hatching enzyme, as pointed out by Freda and Dunson (1985a), is responsible for changes in the VM allowing it to expand in response to the osmotic uptake of water enlarging PVS; further, digestive action of the same enzyme weakens VM facilitating its rupture by muscular action of the embryo. Thus inhibition of this enzyme, which occurs after exposure to low pH or high salt concentrations, will have adverse effects.

Regarding toxic effects of low pH on amphibian development, it has been reported that disruption of ionic regulation is the major cause responsible for the mortality of embryos and tadpoles; loss of sodium has been shown to be one of the prominent effect (Freda and Dunson, 1984, 1985b). Loss of sodium has also been shown to be responsible for mortality of fishes exposed to low pH (Packer and Dunson, 1970). Why older tadpoles were found to be more tolerant of low pH as compared to embryos is inexplicable at present. Presumably, this tolerance was related to the development of functional kidneys and skin, the organs that can control ion influx and efflux.

Results presented here show consequences of short term exposure to altered pHs in *Microhyala ornata* embryos and tadpoles. Effects of long term exposure, from early development through metamorphosis, are being investigated.

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## STUDIES ON THE GROWTH OF THE DESERT TORTOISE (*TESTUDO SULCATA*) IN SUDAN: CHANGES IN MORPHOMETRICS AND BODY WEIGHT FROM HATCHING TO ONE YEAR (0+)

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### ABSTRACT

Changes in morphometrics and body weight during growth was deduced from observations of individual *Testudo sulcata* of known age. A strong positive correlation was found to exist between plastron width ( $r = 0.97$ ), carapace length ( $r = 0.94$ ), carapace width ( $r = 0.94$ ), body weight ( $r = 0.99$ ) and plastron length. Changes in morphometrics and body weight during growth in their first year of life has been investigated. The tortoises increased in size at a rate of  $1.3764 \times 10^{-3} \text{mm day}^{-1}$  (plastron length),  $1.0992 \times 10^{-3} \text{mm day}^{-1}$  (plastron width),  $1.5273 \times 10^{-3} \text{mm day}^{-1}$  (carapace length),  $1.4206 \times 10^{-3} \text{mm day}^{-1}$  (carapace width) and  $5.4519 \times 10^{-3} \text{g day}^{-1}$  (body weight). The values of the intercept (a), regression coefficient (b) and instantaneous growth rate (K) were calculated for *T. sulcata* and from similar growth data in the literature. Their relation to morphological changes in tortoises and turtles have been discussed.

### INTRODUCTION

Current ideas on reptiles life histories suggest that individuals exhibit a series of growth rates during their lives as a function of the source of energy and costs of growth, activity and reproduction (Gibbons, 1968; Wilbur, 1975; Andrews, 1982). This discontinuity in the rate of growth and the endangered status of many reptilian species make identification of growth rates an important area of research, especially in the early stages of the life history.

Although growth, morphometrics and the relative growth of a part in relation to that of the entire organism in many chelonian species have been studied in detail (see Cagle, 1950; Gibbons and Semlitsch, 1982; Meek, 1982; Long, 1984; Mahmoud, El Naeem and Hamad, 1986), early growth has received less attention and none of the published work (King, 1964 on *Testudo graeca*, Blackwell, 1968 on *Kinixys homeana*, Cloudsley-Thompson, 1970 on *T. sulcata*, Tryon and Hulsey, 1977 on *Clemmys muhlenbergi*, Bienefeld, 1979 on *Hydromedusa tectifera*, Davis, 1979 on *Geochelone carbonaria*, Peters and Finne, 1979 on *Geochelone gigantea*, Brown, Marvey and Wilkins, 1982 on *Ereimohelys imbricata* and Inskip, 1984 on *Cuora ambainensis*) has rigorously been quantified. From these data, relative growth rates were calculated and correlations were estimated by Linear regression. This paper describe some aspects of the early growth (0+) in *Testudo sulcata* from hatching to one year after hatching.

### MATERIAL AND METHODS

#### MAINTENANCE

Newly hatched *T. sulcata* (16 from the same clutch) were kept in an enclosure (1.3 x 1.3 x 2m) wired on the

top and back with a shut of glass for viewing on the front. The enclosure contained a shallow concrete pool (0.3 x 0.3m). Food was offered every other day and readily accepted. It consisted of *Medicago sativa* and *Vicus bengalensis*. During February, 1987 the tortoises were unable to feed. This was probably due to a bacterial infection of the mouth. Treatment consisted of a daily dose of 1ml of Rivoclin (Rivopharm, Switzerland) administered orally for one week. The mouth condition responded well, and the animals then began to gain weight rapidly once more.

#### MEASUREMENTS

Each individual was marked in a coded pattern by filling the marginal scute to produce slight notches in the bones. To aid recognition, dark marker paint was placed on the notched marginal scute and renewed mostly at the time of measurement. Records for each individual were kept. These consisted of age, weight in g, (measured with a Mettler balance sensitive to 0.1g), and four linear measurements: plastron length (PL) (greatest length measured at the midline), plastron width (PW) (maximum width along the midline) carapace length (CL) (greatest length measured along the midline) and carapace width (CW) (maximum width along the midline). These measurements were made with a calibrated tape, accurate to 1mm.

#### STATISTICAL ANALYSIS

Regression analysis of plastron length as well as other morphometric measurements, and body weight were carried out in accordance with the following equation.

$$X = a + bY$$

where:

Y is the plastron length in mm; a = the intercept and b the regression coefficient of the morphometric measurement in mm or body weight in g.

Relative growth rates, measured as rate of increase per day, were calculated from the formula (Brody, 1945).

$$K = \frac{\text{Ln}X_i - \text{Ln}X_o}{t_i - t_o}$$

where:

K, is the instantaneous relative growth rate

X<sub>o</sub> and X<sub>i</sub> are the morphometric measurements or body weight at the beginning and end of the age interval t<sub>o</sub> to t<sub>i</sub> Ln, is the base of the natural logarithm.

RESULTS

RELATIVE GROWTH

The reliability of using either plastron length or carapace length as criteria for the measurement of

growth in *T. sulcata* was tested by plotting the two parameters against each other. The linearity of the points (Fig. 1) suggest either parameter can be used to assess growth.

Growth in plastron width and carapace width was investigated in relation to plastron length. The linearity of the points and the regression analysis show a high correlation between PW, CL, CW and the lengthening of the plastron (Fig. 1; Table 1) where 88, 88 and 94 per cent of the points respectively, were accounted for.

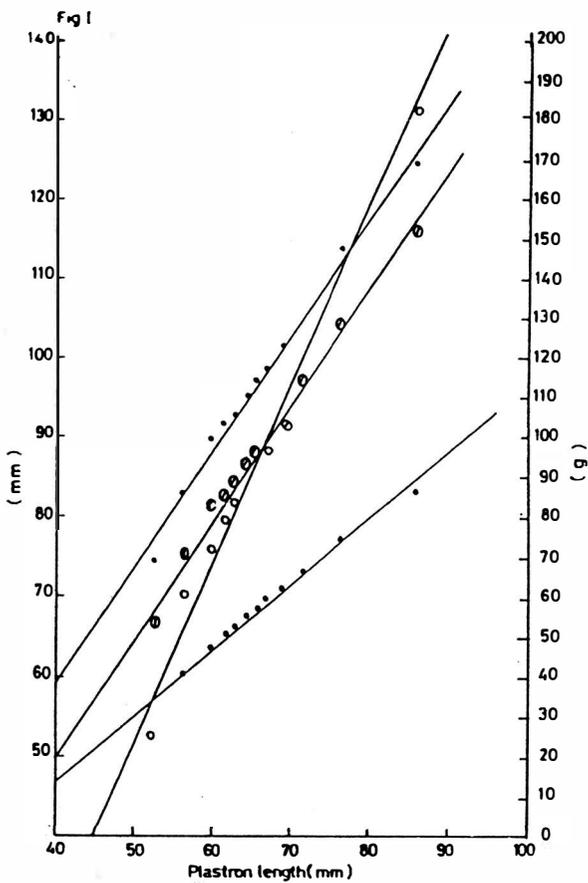


Fig. 1 Relationship between, plastron width (●—●), carapace length (○—○), carapace width (□—□), body weight (○—○) and plastron length in O+ *T. sulcata*.

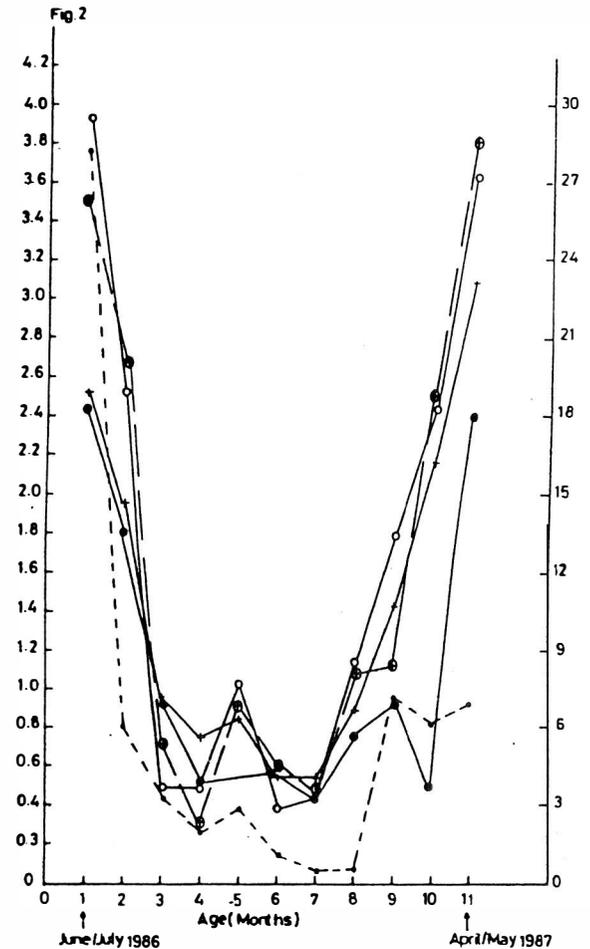


Fig. 2 Instantaneous relative growth rate of plastron length (+—+), plastron width (●—●), carapace length (○—○), carapace width (⊕—⊕) between when first measured in June, 1986 and last measured in May, 1987 as a function of age in O+ *T. sulcata*.

Parameter	Intercept (a)	Regression coefficient (b)	Correlation coefficient (r)	r <sup>2</sup>
Carapace length	-8.8351	1.4757	0.94	88
Carapace width	-3.3556	1.5284	0.94	88
Plastron width	14.8838	0.8121	0.97	94
Body weight	-201.64338	4.5262	0.99	98

TABLE 1: Results of the regression analysis of some morphometric measurements (mm) and of body weight (g) on plastron length (mm) of *T. sulcata*.

The regression between plastron length and body weight (Fig. 1) expressed by the equation:

$$W = 201.6438 + 4.5262 \times PL$$

indicates that body weight increased relatively faster than plastron length, because the regression coefficient (b) is greater than 1 (Table 1). The correlation is very highly significant and 98 per cent of the points are accounted for.

The plot of the monthly instantaneous relative growth rates (Fig. 2) shows that carapace length and width had a greater overall relative rate of growth than plastron length and width. However, the inconsistency in this trend throughout the year is probably due to the formation of a carapace of the same shape.

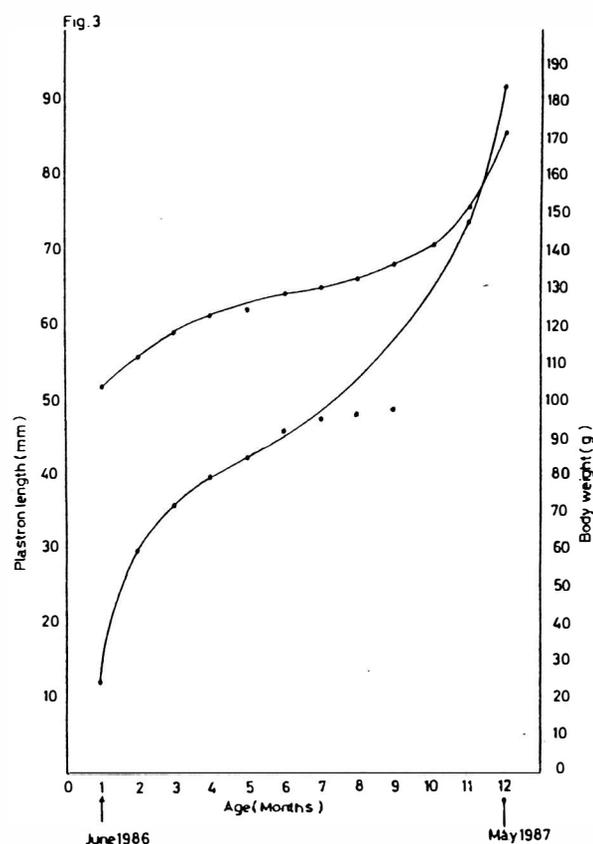


Fig. 3 Relationship between plastron length (○—○), body weight (●—●) of O+ *T. sulcata* and time in months during June 1986 and May 1987.

#### ABSOLUTE GROWTH

When the mean plastron length and mean body

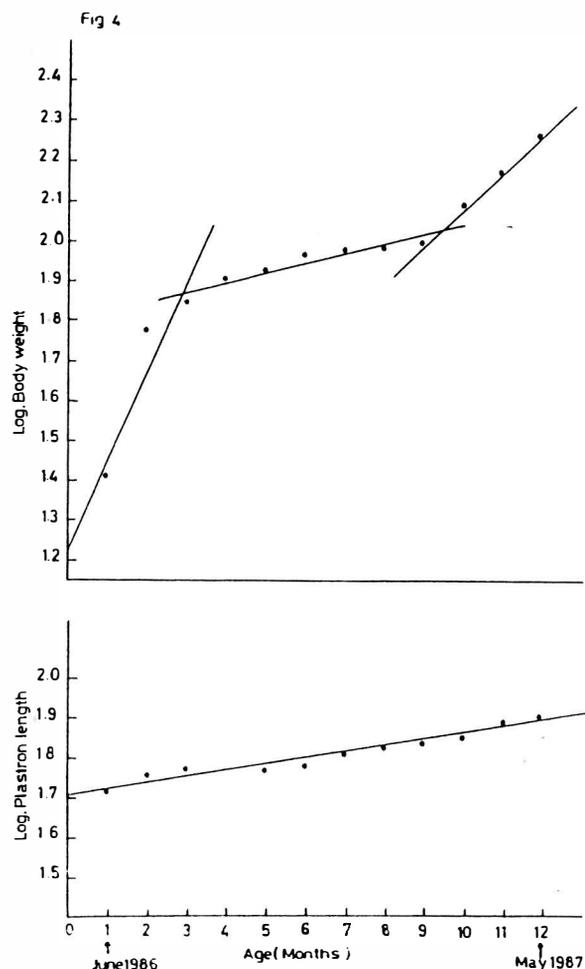


Fig. 4 Relationship between the growth in plastron length (○—○), body weight (●—●) and time (months). The growth modes are represented by the regression lines.

weight were plotted against age on a linear scale, a sigmoid growth pattern was obtained (Fig. 3). The plot of the logarithmic value of the mean plastron length and the mean body weight against age, straighten the curve for plastron length (Fig. 4).

A separate regression line has to be calculated for each of the three growth modes obtained for body weight (Fig. 4 and Table 2). The points of intersection of the regression lines were observed to lie between days 84 and 282 after hatching. The three regression were highly significant ( $P < 0.01$ ) and most of the points were accounted for by the three lines.

Parameter	Intercept (a)	Regression coefficient (b)	Correlation coefficient (r)	$r^2$
Plastron length	1.7153	0.0154	0.97	94
Body weight				
First growth mode	1.2346	0.2241	0.94	88
Second growth mode	1.8091	0.0226	0.96	92
Third growth mode	1.2338	0.0856	0.99	98

TABLE 2: Results of regression analysis for the relationship between plastron length (X, log mm) and body weight (X, log g) with age (Y, months) in *T. sulcata*. The regression following the equation.

$Y = a + b \log X$ , where a and b are constants.

Species	No. of animals	Duration $t_0-t_1$ in days	Body weight $g. day^{-1}$ $10^{-3}$	Plastron length $mm day^{-1}$ $10^{-3}$	Plastron width $mm day^{-1}$ $10^{-3}$	Carapace length $mm day^{-1}$ $10^{-3}$	Carapace width $mm day^{-1}$ $10^{-3}$	Reference
<i>Geochelone carbonaria</i>	15	76	5.69	—	—	2.01	—	Davis, 1979
<i>Geochelone gigantea</i>	8	96	8.37	3.54	2.72	3.92	—	Peters and Fine, 1979
<i>Kinixys homeana</i>	3	95	13.25	—	—	—	—	Blackwell, 1968
<i>Testudo graeca</i>	5	12	5.72	2.43	—	—	—	King, 1964
<i>T. sulcata</i>	1	18	10.30	—	—	2.41	1.31	Cloudsley-Thompson, 1970
<i>T. sulcata</i>	16-9	365	5.45	1.38	1.09	1.53	1.42	Present work
<i>Clemmys muhlenbergii</i>	2	367	6.36	—	—	2.36	—	Tryon and Hulse, 1977
<i>Hydromedusa tectifera</i>	7	122	7.27	—	—	2.36	2.22	Benefield, 1977
<i>Eretmochelys imbricata</i>	103	365	—	—	—	8.93	—	Brown <i>et al.</i> , 1986
<i>Curo amboinensis</i>	1	199	5.52	—	—	1.86	1.98	Inskeep, 1984

TABLE 3: Calculated Instantaneous growth rate (k-value) for some chelonians (present work and literature)

Growth in the weight of hatchling *T. sulcata* per unit time was characterised by an initial fast growing period at a rate of  $11.46 \times 10^{-3} g day^{-1}$  until about August, followed by a slow growing rate of  $1.50 \times 10^{-3} g day^{-1}$  until about February and a fast growing rate of  $5.13 \times 10^{-3} g day^{-1}$  by the time when the animals are one year old (Table 2 and 3). The growth in plastron length followed the same trend and during these period a rate of  $1.52 \times 10^{-3} mm day^{-1}$ ,  $0.65 \times 10^{-3} mm day^{-1}$  and  $1.85 \times 10^{-3} mm day^{-1}$  was computed.

### DISCUSSION

During the growth of newly hatched *T. sulcata* a strong positive correlation was found between plastron length and other morphometric measurements (Table 1). Similar findings have been reported between plastron length and carapace length in young hatchling *Platemys platycephala* ( $r = 0.99$ ) by Ernst and Lovich (1986) and in adult of *Gopherus agassizi* ( $r = 0.99$ ) by Medica, Bury and Turner (1975). They have also been calculated from the data of Peters and Finne (1979) in one year old *G. gigantea* ( $r = 0.93$ ). Plastron length can therefore be used as the independent variable in relative and absolute growth studies, due to its relatively constant rate of growth. Ernst (1977) and

Ernst and Lovich (1986) stated that straight line carapace measurement includes much hidden growth masked in its curvature.

Mathematical models based on plastron length could be misleading if differences in plastron length between males and females exist. Although plastron length dimorphism has been demonstrated in several chelonian species (Berry and Shine, 1980; Branch, 1984), the clearest sex discrimination functions (tail length and anal region measurements) failed to distinguish the sex of O+ *T. sulcata* (Mahmoud and Mustafa, 1987). In the present study all of *T. sulcata* examined were small in size (under 106mm plastron length) and can only safely be classified as juveniles. Therefore, the plastron length is clearly a useful measurement for describing the growth of O+ *T. sulcata*.

The present study showed that in *T. sulcata* the body weight increases relatively faster than plastron length ( $b > 1$ , Table 1). The calculated regression coefficient values ( $b$ ) showed that the O+ old tortoises tend to increase more in weight than in length when compared with O+ old turtles (Table 4). This might be due to relatively faster growth of tortoises as that they become dome-shaped with increase in size, while turtles tends to remain flat. Similar observations have

Species	Intercept (a)	Regression coefficient (b)	Correlation coefficient (r)	Reference
Tortoises:				
<i>Geochelone carbonaria</i>	-125.7299	2.9536	0.98	Davis, 1979
<i>Geochelone gigantea</i>	-150.3738	3.7163	0.91	Peters and Finne, 1979
<i>T. sulcata</i>	-224.0133	4.8143	0.97	Present work
Turtles:				
<i>Hydromadusa tectifera</i>	-23.1891	0.8578	0.99	Benefield, 1977
<i>Clemmys muhlenbergii</i>	-25.3801	1.0118	0.98	Tryon and Hulse, 1977
<i>Cure ambolmensis</i>	-37.3781	1.2047	0.93	Inskeep, 1984

TABLE 4: Regression analysis of carapace length (mm) and body weight (g) describing the early growth in some chelonians.

been reported in *E. imbricata* by Brown *et al.* (1982). Mosiman (1958) and Long (1984) reported that the length of the flat soft-shell turtles had greater intercept values as opposed to other, more domed species. The same opinion hold true when the intercept value of *T. sulcata* (present study) and calculated values for tortoises and turtles (literature) are compared (Table 4).

In *T. sulcata* late summer and early winter account for the lower K-values during mid-August to mid-January. Medica *et al.* (1975) found that *G. agasszi* grew most rapidly during the spring (mid-April) and early summer (first week of July). However, the discrepancy of the K-value (present work and literature) is due to difference in the species, their zoogeography, the duration of the study and number of animals involved (Table 3).

Additional long term growth data are required to verify whether the fluctuation in K-value is due to seasonality and/or some physiological factors that need to be investigated. To cast light on these problems, records for the 1986 hatchling will continue and the 1987 hatchling are now studied in terms of the impact of environmental factors and food quality on growth of *T. sulcata*.

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## DISTRIBUTION AND STATUS OF CREASER'S MUD TURTLE, *KINOSTERNON CREASERI*

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### ABSTRACT

Field studies on the Yucatan peninsula in 1985 and 1987 revealed 38 new localities for Creaser's mud turtle. This turtle typically inhabits shallow, temporary pools in undisturbed forest. It apparently estivates below ground during most of the dry season, and is active primarily during the wet season when forest pools are present. It is not a usual inhabitant of permanent water microhabitats (e.g. cenotes). Populations appear to be most dense in Quintana Roo, where deforestation has not been as intense as in northern Campeche and Yucatan. These turtles eat mainly animal matter. Females exhibit a 'tropical' reproductive pattern, producing few, large eggs during the middle of the wet season (August-October). Juvenile growth rates are rapid, but adults grow slowly and are not large in comparison to related congeners. Males are aggressive toward other males and only one was found in any single pool or pond.

### INTRODUCTION

*Kinosternon creaseri* (Creaser's mud turtle; Fig. 1), described 51 years ago (Hartweg, 1934), is restricted to the Yucatan Peninsula of Mexico, and is one of the most poorly known Mexican turtles. Previously only 70 specimens were known from 18 localities (Iverson, 1983; APPENDIX A), and the species was listed as RARE in the IUCN Amphibia-Reptilia Red Data Book (Groombridge, 1982). In evidence of its rarity (or secretiveness), only two specimens were collected by Dr. Julian Lee of the University of Miami during nine months of herpetological field work on the Peninsula (Lee, 1980). Similarly, Himmelstein (1980) found only a single specimen during six trips totalling more than 53 field days over five different months. Despite intensive trapping I captured no specimens during my own Yucatan field work in April 1981.

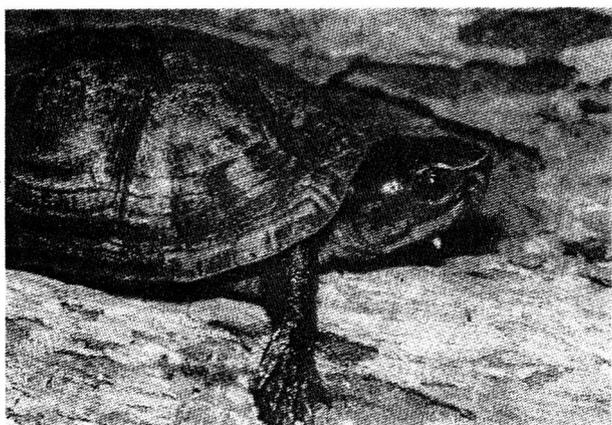


Fig. 1 Adult male *K. creaseri* (CL 124mm) from Quintana Roo, 21.9km N Playa de Carmen turnoff on coastal Hwy 307. Note the strongly hooked beak characteristic of this species.

### METHODS

Because so little is known about the distribution, natural history, and status of this species, I surveyed the Yucatan peninsula in 1985 and 1987. All types of aquatic habitats (e.g. cenotes, lakes, temporary and permanent ponds) were trapped, seined, or, if shallow and relatively clear, searched visually. Although *K. scorpioides* and *K. leucostomum* were often captured in traps, only a single *K. creaseri* was ever trapped. Seining was also relatively unproductive; only two *K. creaseri* were seined. The most effective field capture technique involved thorough visual searches of shallow forest pools and roadside ponds with collection by hand. Driving roads during heavy rainstorms produced the most turtles, although little could be determined about natural microhabitats. Every one of the previously known localities (APPENDIX A) was visited except one that could not be located (Vivienda de Platanal). Because of the potentially threatened status of the species, most specimens observed in the field were released.

### RESULTS AND DISCUSSION

Despite the documentation of 38 new localities, I was unable to extend the range of *K. creaseri* beyond that previously known (Fig. 2; APPENDIX A). The species range is (or was) probably continuous over much of the Yucatan peninsula, except in the northwestern quadrant, where it may be too dry for it to exist. Deforestation and the use of low areas for agriculture have apparently reduced populations in some areas, especially in the northern and western portions of the peninsula.

Future field work should be concentrated in southern Campeche and southern Quintana Roo, in

particular the rectangular area between Dzibalchen, Escarcega, Felipe Carillo Puerto, and Chetumal.

*Kinosternon creaseri* is an average sized mud turtle, and males grow slightly larger than females (Table 1).

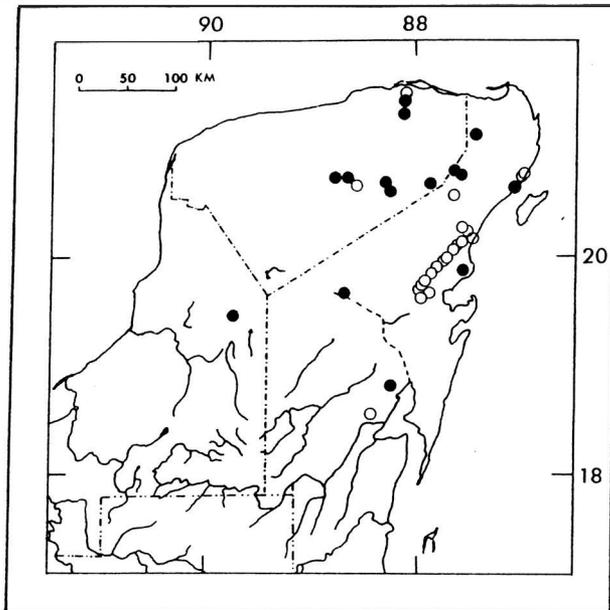


Fig. 2 Distribution of Creaser's mud turtle, *Kinosternon creaseri*, on the Yucatan Peninsula of Mexico. Solid circles represent previously known localities; open circles are new localities or previous ones confirmed during this study. Each symbol represents at least one locality.

Carapace length (CL in mm) is related to wet body mass (BM in g) by the equation  $BM = 0.0006608 CL^{2.649}$  (N = 20; CL range = 25.9 to 124.0;  $r = 0.998$ ;  $p < 0.0001$ ). Plastron length averages 94.7% of CL in males, 97.1%

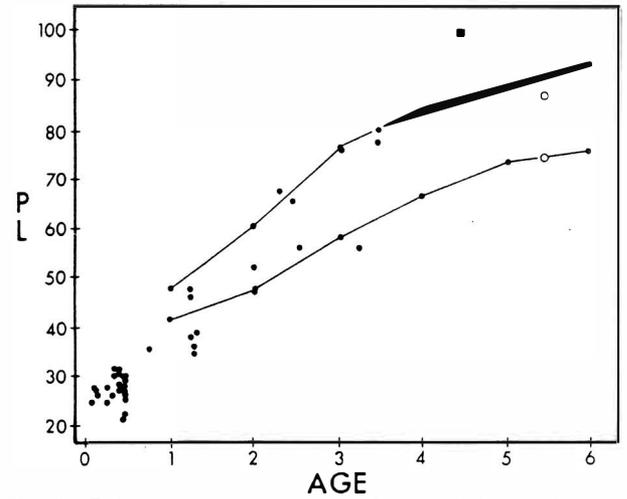


Fig. 3 Relationship between actual age and plastron length (PL in mm) for male (N = 1; solid square), female (N = 2; open circles), and juvenile (N = 56; solid circles) Creaser's mud turtles with obvious plastral annuli. Actual age was calculated by adding the proportion of the year that had passed (assuming growth from 1 June to 1 December) to the number of plastral annuli (excluding the one from the turtle's first winter). Solid lines connect mean estimated winter plastron lengths of turtles from Table 2. Each symbol represents at least one turtle.

Species	Male				Female		
	MFR	N	Mean CL	Range	N	Mean CL	Range
<i>Kinosternon acutum</i>	0.953	20	91.8	78.4-100.5	20	96.3	77.3-115.6
<i>K. alamosae</i>	1.083	36	113.2	83.5-127.2	19	104.5	89.2-120.3
<i>K. augustipons</i>	0.904	11	94.0	81.2-109.0	3	103.9	87.0-116.8
<i>K. baurii</i>	0.914	101	83.7	72.0-103.8	52	91.6	69.0-115.3
<i>K. carinatum</i>	1.069	17	119.4	86.5-161.7	16	111.6	81.3-138.0
<i>K. creaseri</i>	1.077	22	115.2	96.0-124.9	17	107.0	89.1-121.5
<i>K. dunnii</i>	1.368	1	169.0	—	4	123.5	91.8-148.2
<i>K. flavescens flavescens</i>	1.103	158	115.5	78.0-141.9	137	104.7	76.6-135.1
<i>K. flavescens arizonense</i>	1.085	52	145.9	103.0-181.3	97	134.5	95.5-167.3
<i>K. flavescens durangoense</i>	1.167	5	153.0	134.0-182.9	4	131.1	117.9-144.6
<i>K. herrerae</i>	1.123	46	135.6	92.5-166.4	60	120.8	90.9-146.0
<i>K. hirtipes</i>	1.088	312	130.5	80.0-181.8	244	120.5	73.5-152.0
<i>K. integrum</i>	1.137	171	146.5	82.1-197.0	220	128.9	77.6-168.4
<i>K. leucostomum</i>	1.095	139	124.6	96.3-170.8	138	113.8	84.5-166.4
<i>K. minor</i>	0.954	310	82.3	46.9-124.3	341	86.3	47.1-132.9
<i>K. oaxaca</i>	1.138	15	138.9	93.0-175.1	15	122.1	94.9-140.5
<i>K. odoratum (Indiana)</i>	0.972	44	85.8	63.9- 95.5	26	88.3	65.0- 99.4
<i>K. scorpoides cruentatum</i>	0.993	69	114.4	86.8-138.8	82	115.2	84.2-147.5
<i>K. scorpoides abaxillare</i>	1.041	16	123.0	88.1-149.0	35	118.2	88.4-153.3
<i>K. sonoriense</i>	0.971	78	114.6	80.8-154.0	71	118.0	79.9-160.4
<i>K. subrubrum hippocrepis</i>	0.931	26	86.2	76.6- 95.4	31	92.5	80.0-111.3
<i>K. subrubrum steindachneri</i>	0.993	45	91.0	75.0-114.3	51	91.6	77.0-107.0
<i>K. new species (Jalisco and Colima)</i>	1.077	20	111.5	82.1-153.7	31	103.5	86.5-128.8

TABLE 1: Sexual dimorphism in kinosternine turtles. Ratio of mean male to mean female carapace length (CL) is included (MFR). Only externally sexable (not necessarily mature) turtles included.

in females, and 85.8% in small juveniles. Sexing of subadults >90mm CL is possible, based on tail length (long in males).

Based on counts of plastral annuli and the assumption that a single annulus is produced each year (see Ernst *et al.*, 1973), juvenile growth is very rapid (Fig. 3), and males appear to grow faster than females by their second year (Table 2). However, because turtles from different localities and years were included in this analysis, the potential for error exists. Six turtles captured early during their first year grew to an average of 88.3mm CL (range 84-93) and 80.9mm PL (range 78-86) during two years in captivity. This rate is significantly faster than estimates for natural growth, but the captives had water and food available year-round.

*Kinosternon creaseri* is easily confused with some peninsular specimens of *K. scorpioides*. However, the former can be reliably identified in the field by its aggressive behaviour, more pungent musk, and curved seam between the scutes of the plastral hindlobe and those of the fixed mid-portion of the plastron. *K. scorpioides* on the peninsula nearly always withdraws and closes its shell on capture, has a much less pungent odour, and has a straight seam across the anterior margin of the femoral scutes.

*Kinosternon creaseri* might also be confused with its probable sister taxon, a nearly parapatric species with similar body size and habits, *Kinosternon acutum* (Iverson, 1980). The latter species is known (in Belize, Corozal District, 2mi. N Orange Walk; UU 9449) from within 45km of the nearest record for *K. creaseri* (Quintana Roo, 13mi N Chetumal; SM 11448), and their ranges may overlap in southern Campeche and Quintana Roo. The difficulty in distinguishing them is evidenced by Duellman's (1965) misidentification of KU 70928 from 11km S Champoton, Campeche as

*creaseri* rather than *acutum*, and my own misidentification (Fig. 2 in Iverson, 1980) of SM 11448 as *acutum* rather than *creaseri*. However, based on the results of a discriminant analysis of morphometric character ratios (Fig. 4; method after Iverson, 1981), they can be distinguished based on the usually straight anterior margin of the plastral hindlobe (usually curved in *creaseri*), the longer interabdominal seam (AB) and bridge length (BL), and the wider anterior plastral lobe (measured across plastron at level of junction of plastral margin and humeral-pectoral seams; PWA) found in *K. acutum*. BL/PWA averages 0.87 in female (range 0.75-0.97; N = 27) and 0.83 in male (0.77-0.93; N = 25) *acutum*, and 0.71 in female (0.64-0.79; N = 11) and 0.70 in male (0.60-0.77; N = 15) *creaseri*. AB/PWA averages 0.81 in female (0.70-0.94) and 0.79 in male (0.73-0.89) *acutum*, and 0.71 in female (0.64-0.78) and 0.70 in male (0.62-0.77) *creaseri*.

Like the results presented in Fig. 4, discriminant analysis of the same morphometric character ratios for *K. creaseri* alone suggests that specimens from the state of Yucatan differ significantly from those from Quintana Roo and Campeche. In the female analysis only the ratio of the width of the plastral hindlobe at the level of the junction of the plastral margin and the femoral-anal seams (PWD) to carapace length varied significantly among states. Females from Yucatan state had wider plastral hindlobes (mean PWD/CL = 0.36 in eight turtles from Yucatan, 0.33 in three from Quintana Roo). In the male analysis, the ratios PL/CL, AB/CL, and PWC/CL varied significantly among states. Males from Yucatan state had longer plastrons (mean PL/CL = 0.96 in nine turtles from Yucatan, 0.93 in six from Quintana Roo, and 0.94 in one from Campeche) and longer interabdominal seams (mean AB/CL = 0.29 in Yucatan, 0.27 in Quintana Roo, and 0.28 in Campeche). The Campeche male also had a wider

MALES					FEMALES			
Age	N	Mean PL	Range	% increase from previous year	N	Mean PL	Range	% increase from previous year
0?	14	24.8	22.1- 27.8					
1?	6	45.5	37.5- 53.6					
1	4	47.1	41.2- 51.4	89.9	5	40.5	37.1-44.0	66.5
2?	5	55.2	50.1- 59.0					
2	4	60.1	52.0- 63.5	27.6	5	47.2	44.8-51.0	16.5
3?	2	76.3	74.6- 77.9					
3	3	75.8	68.1- 83.8	26.1	5	57.5	52.3-69.5	21.8
4	4	84.1	72.7- 96.7	10.9	5	65.8	60.5-77.6	14.4
5	3	86.8	74.8-100.6	3.2	5	72.6	65.1-84.0	10.3
6	3	93.5	83.0-107.0	7.7	3	75.9	69.1-81.9	4.5
7	2	89.9	86.6- 93.2	—	3	82.6	73.7-90.3	8.8
8	2	94.0	91.5 -96.5	4.6	2	86.3	83.7-88.9	4.5
9	2	97.7	96.7- 98.7	3.9	2	90.4	84.4-96.3	4.8

TABLE 2: Growth (plastron length in mm) of *Kinosternon creaseri* calculated from four males, five females, and 14 juveniles with obvious abdominal scute annuli. Ages 0?, 1?, 2?, and 3? indicate unsexable turtles of 0, 1, 2, and 3 growing seasons of age, respectively.

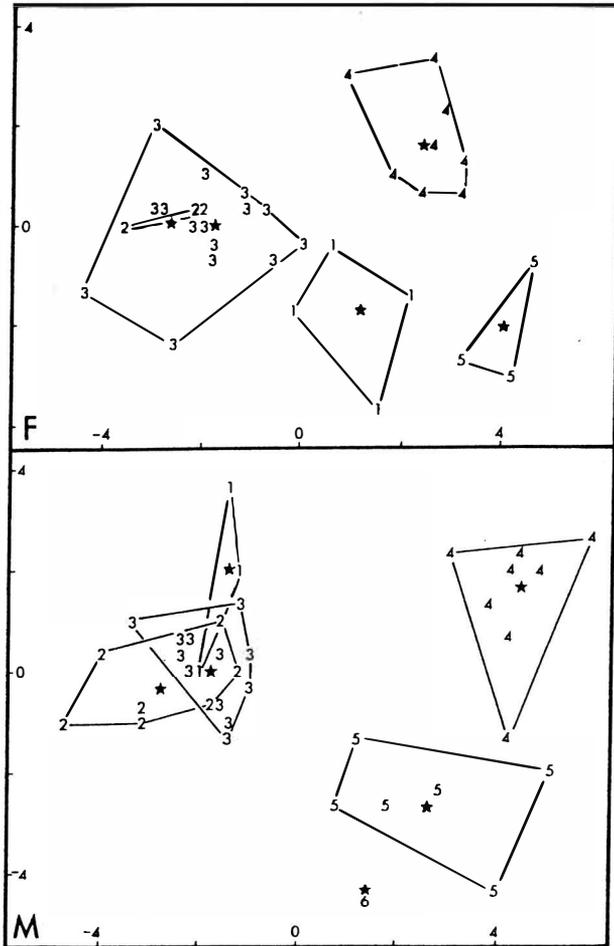


Fig. 4 Plots on the first two canonical axes of population means (stars) of female (above) and male *Kinosternon acutum* (populations 1-3) and *K. creaseri* (4-6) produced by discriminant analysis (SPSS-X program) based on 23 character ratios. Population codes are 1, Veracruz and Oaxaca; 2, Tabasco; 3, Guatemala and Belize; 4, Yucatan; 5, Quintana Roo; and 6, Campeche. First two axes account for 69.4 and 19.5% of the variation, respectively, for females; and 66.1 and 19.5% for males.

plastral hindlobe measured across its anterior margin (mean PWC/CL = 0.35 in Yucatan, 0.35 in Quintana Roo, and 0.36 in Campeche).

Colouration also varies geographically. Live specimens from Quintana Roo are generally darker (blacks to dark browns versus medium browns), with lighter pigmented areas on the head and neck coloured pale yellow. However, specimens from near Piste in central Yucatan are much lighter with bright yellow markings on not only the neck and sides of the head, but also on the anterior surfaces of the forelegs. In spite of this apparently significant geographic variation, I do not advocate describing subspecies until more material is available and patterns of variation better understood.

Creaser's mud turtles were found in shallow (<0.5m), temporary forest pools (13), temporarily filled (<0.6m deep) borrow pits or roadside ponds (25), or on roads during rainstorms (26, including 23 first year turtles). They were not found in cenotes or other permanent water habitats, although these habitats

were trapped and/or searched intensively. However, they must occasionally visit these habitats, because specimens have apparently been taken in them (e.g. UMMZ 73083 and 73086; APPENDIX A). With three exceptions only one *K. creaseri* was found in any single pool or pond. In two cases, each in a shallow forest pool, a male and female were found together in the same pool (one pair in copula on 17 August). Two first year turtles were also found together in the same pool. Microhabitat densities are thus probably not ever very great (see below).

Based on field observations, the species seems to be most common in the northern two-thirds of Quintana Roo. Broad sympatry between *K. creaseri* and *K. scorpioides*, *K. leucostomum*, *Rhinoclemmys areolata*, *Terrapene carolina yucatanica*, and *Trachemys scripta* is known (Smith and Smith, 1980); however microsympatry between any of the latter five and *K. creaseri* has not previously been documented. We did observe *K. scorpioides* and *R. areolata* in similar pools as close as 25m to those where *K. creaseri* was found, but actually found *K. creaseri* in the same pond with another species of turtle only twice.

The first was a 20 by 15m roadside pond (max. depth 0.75m) in a cattle pasture adjacent to a sinkhole, and contained at least one *K. scorpioides*, one *K. creaseri*, 53 *T. scripta* (estimated biomass at least 135kg/ha!), and obviously introduced cichlid fish. This was also the only site where *K. creaseri* was found in water supporting a fish population, even though it was unnatural. The second site was also a roadside pond (25m x 15m x 1m maximum depth) in a natural depression in a second growth forest. A single trap baited with sardines and set for four hours produced one *K. scorpioides*, one *K. creaseri*, and one *K. leucostomum*.

Within the range of *K. creaseri* we observed *Trachemys* at nine new localities, *Rhinoclemmys* at 13, *K. leucostomum* at two, and *K. scorpioides* at 21. Like the latter two species, *Rhinoclemmys* probably also occurs microsympatrically with *K. creaseri* on occasion. In Quintana Roo we found hatchlings of *Rhinoclemmys* and *K. creaseri* on the road within 200 and 600 metres of each other at four localities, and a subadult *Rhinoclemmys* on the road within 50m of the nearest pond, which contained *K. creaseri*.

Creaser's mud turtles are apparently primarily carnivorous, since they defecated mainly insect parts and snail shells. However, occasional individuals defecated palm seeds. Captives ate only animal matter.

Creaser's mud turtle apparently spends most of the year buried underground. All but four collection records (Himmelstein, 1980, UMMZ 81539-40 and USNM 46271; collected in February or March) fall between June and December (the rainy season on the Yucatan peninsula), and I was unable to collect the species during intensive field work in April 1981 at the height of the dry season. Although estivation sites are unknown, turtles probably bury below leaves into the moist humus layer of the forest floor as pools dry up during the fall and winter. However, the February/March records suggest that turtles may reemerge whenever temporary pools are filled by rains.

The activity season apparently may be severely reduced during dry years. Although we found turtles fairly abundant in central and northern Quintana Roo in August 1985 and in central Quintana Roo in August 1987, the southern part of the state was very dry. Most roadside pools that obviously would normally hold water during the wet season were dry, and *Kinosternon*-sized turtle tracks suggested that turtles had moved into the nearby forest. Whether or not it is ever dry enough that turtles are forced to estivate through a wet season (i.e. be inactive for 18 months or longer) is not known. Other Mexican *Kinosternon* (at least *flavescens* and probably *atamosae*), in drier habitats, are capable of remaining inactive during such drought years (Iverson, 1988 and 1989).

Based on plastral annuli, female Creaser's mud turtles reach maturity at body sizes between 110 and 115mm CL and apparent ages between 10 and 15 years. Two dissected females of 106 and 108mm CL (with between 16 and 18 and ca. 10 plastral annuli, respectively) were immature, with no follicles over 2mm diameter. However, plastral annuli may not be perfectly correlated with age. The only adult female dissected (116mm CL, 207gm BM, and at least 17 plastral annuli on 25 August) contained a single, relatively huge egg (38.2 x 19.1mm; 8.9gm), its corresponding corpus luteum, and enlarged follicles of 19 and 13mm diameter. The latter suggest that two or three clutches of a single egg each might be deposited annually. Nest sites or nesting behaviour have not been observed.

This species exhibits a typical 'tropical' pattern of reproduction (c.f. Moll and Legler, 1971), with multiple, small clutches of large eggs being produced. Reproductive effort, as measured by wet clutch versus wet body mass, is relatively low in the single dissected female *K. creaseri* (4.3%) compared to that of most other *Kinosternon* (average ca. 10%); however, the average expenditure per progeny (EPP; wet egg versus wet body mass) is among the highest of the subfamily (4.3%). Typical kinosternines average 2%, and in some species EPP is as low as 0.4%. Only *K. acutum*, *K. augustipons* and *K. leucostomum* produce such relatively large eggs among the kinosternines (Iverson, unpublished), with EPP also near 4%.

Densities are very difficult to calculate because turtles typically inhabit complex mosaics of shallow forest pools. In addition during rainy weather they apparently migrate among pools. Ticks were found on the neck of the specimen from Dzibalchen, Campeche (KU 75644), suggesting that terrestrial movements are common. The most surprising demographic observation is the abundance of first year turtles among the specimens previously collected (at least 25 of 68), as well as observed during my field work (30 of 54). Hatchling kinosternids are typically not commonly encountered.

Except in permanent water habitats, *K. creaseri* would appear to be the most abundant turtle on the Yucatan. We captured 28 *K. scorpioides* (including five juveniles and two hatchlings), 12 *Rhinoclemmys* (seven juveniles and five hatchlings), and 54 *K. creaseri*

(including 12 juveniles and 30 hatchlings) in other habitats.

Creaser's mud turtles are very aggressive in comparison to congeners. On capture these turtles (even hatchlings) did not withdraw their heads and close their shells, but rather attempted to bite their captor (often viciously). The strong, prominent beak diagnostic of the adult of this species is probably an adaptation for aggressive encounters, rather than for feeding. At least six of the 15 subadult or adult turtles captured exhibited eroded carapace margins, probably due to aggressive encounters. When other adults were placed in the same container as an adult male they showed evidence within a day of biting along the anterior margins of their shells. Males also attacked *K. scorpioides* in a smaller manner. Even hatchlings exhibited intraspecific aggression. In captivity one would frequently mount another (in a typical kinosternid copulatory position) and attempt to bite the head and anterior margin of the other's shell. In the only case where two first year turtles were found in the same pool, the slightly larger individual was mounted on the shell of the smaller one, biting at it exactly as observed in captivity.

Because of the observations above, and the fact that only one male was ever found in any single pool in the field, it is believed that this species may be territorial. A male that is aggressive enough to drive other males from its forest pool would have unlimited access to food and females in that pool. Whether their aggression is directed interspecifically in the field is not known.

One additional behavioural difference between *K. creaseri* and *K. scorpioides* was observed. Hatchlings of the latter species frequently basked in captivity, but those of the former almost never did.

Although Creaser's mud turtle is much more common than previously thought, its preferred natural microhabitat (forest floor pools) is threatened due to intensive deforestation on the Yucatan peninsula. Removal of the forests increases evaporation, resulting in fewer pools of water. In addition, the basins that previously held water are usually the first to be exploited for cultivation because they are lower, wetter, and have richer soil. Therefore the status of this poorly known turtle should be monitored regularly.

#### ACKNOWLEDGEMENTS

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- 1.5km S, 7km E Pueblo Nuevo X-Can: KU 70921-22.  
3.8km N Kantunil Kin: KU 171402.  
21.9km N Playa del Carmen turnoff on coastal Hwy 307: JBI.  
19.3km N Playa del Carmen turnoff on coastal Hwy 307: JBI.  
Playa del Carmen: Himmelstein, 1980(81).  
0.1km E Lago Coba: JBI (2 specimens).  
0.3km S Lago Coba: JBI.  
0.7km S Lago Coba: JBI (2 specimens).  
1.9km S Lago Coba: JBI.  
2.1km S Lago Coba: JBI.  
7.7km N Hwy 307 on Coba Road: JBI (4 specimens).  
2.9km N Coba Road on Hwy 307: JBI.  
1.8km N Coba Road on Hwy 307: JBI.  
1.1km N Coba Road on Hwy 307: JBI (2 specimens).  
Coast road south of Tulum, 0.5km N of Tulum bypass turnoff to West: JBI.  
8.9km SW Coba turnoff on Hwy 307 (= 87.3km NE of Felipe Carillo Puerto square): JBI.  
18.0km SW Coba turnoff on Hwy 307: JBI.  
22.3km SW Coba turnoff on Hwy 307: JBI (2 specimens).  
22.4km SW Coba turnoff on Hwy 307: JBI.  
24.6km SW Coba turnoff on Hwy 307: JBI.  
24.8km SW Coba turnoff on Hwy 307: JBI.  
24.9km SW Coba turnoff on Hwy 307: JBI (2 specimens).  
27.0km SW Coba turnoff on Hwy 307: JBI.  
27.5km SW Coba turnoff on Hwy 307: JBI.  
36.6km SW Coba turnoff on Hwy 307: JBI.  
37.1km SW Coba turnoff on Hwy 307: JBI.  
37.9km SW Coba turnoff on Hwy 307: JBI.  
41.0km SW Coba turnoff on Hwy 307: JBI.  
41.8km SW Coba turnoff on Hwy 307: JBI.  
42.7km SW Coba turnoff on Hwy 307: JBI.  
49.1km SW Coba turnoff on Hwy 307: JBI.  
50.0km SW Coba turnoff on Hwy 307: JBI.  
50.9km SW Coba turnoff on Hwy 307: JBI.  
52.7km SW Coba turnoff on Hwy 307: JBI  
53.4km SW Coba turnoff on Hwy 307: JBI  
61.1km SW Coba turnoff on Hwy 307: JBI  
70.6km SW Coba turnoff on Hwy 307: JBI.  
76.2km SW Coba turnoff on Hwy 307: JBI.  
83.9km SW Coba turnoff on Hwy 307 (= 12.3km NE Felipe Carillo Puerto square): JBI.  
7.8km ENE of Felipe Carillo Puerto square on Vigia Chica Road: JBI.  
17.15km ENE of Felipe Carillo Puerto square on Vigia Chica Road: JBI.  
29.1mi E Felipe Carillo Puerto: KU 157671.  
0.5mi E Presumiada: CU 48020.  
13.4mi SW Limones: KU 157670.  
13mi N Chetumal: SM 11448.

## APPENDIX A

## KNOWN LOCALITIES OF CREASER'S MUD TURTLE IN MEXICO

Specimen acronyms are BMNH, British Museum of Natural History; CM, Carnegie Museum of Natural History; CU, University of Colorado; FMNH, Field Museum of Natural History; JBI, John Iverson field observations; KU, Museum of Natural History, University of Kansas; MCZ, Museum of Comparative Zoology, Harvard University; SM, Strecker Museum, Baylor University; UAZ, University of Arizona; UMMZ, University of Michigan, Museum of Zoology; USNM, United States National Museum; and UU, University of Utah. Localities arranged generally north to south within state.

## CAMPECHE

Dzibalchen: KU 75644.

## QUINTANA ROO

Vivienda de Platanal: FMNH 29131 (locality not findable).  
Pueblo Nuevo X-Can: UU 9450, CU 29178-93,  
KU 70918-20, 70930, CM 40118-20.

## YUCATAN

37.1km N Tizimin square: JBI.  
13mi S Rio Lagartos: CU 45951.  
12mi N Tizimin: CU 29996.  
1.6km SW Catzin: KU 171403.  
1.5mi S Libre Union: CU 29194.

Chicken Itza: USNM 46271, FMNH 27270, 36605, MCZ 46501 (formerly UMMZ 73088; paratype), UMMZ 73085 (paratype), 73089 (paratype), 73210 (paratype), 73087 (paratype), 81539-40.  
 Chicken Itza, Trail Thompson's Cenote: UMMZ 73083 (paratype).  
 Chicken Itza, 2mi S Hacienda: UMMZ 73084 (paratype).  
 Chicken Itza, XCan Cenote: UMMZ 73086 (paratype).

Chicken Itza, Imi S Hacienda (type locality): UMMZ 73090 (holotype).  
 Piste: KU 70923-27, 70929, 70931, UAZ 28839, 28843, 28846-47, 28849-50, CU 18222-23, 16128, JBI (7 specimens).  
 8mi W Vallodolid: CU 45949.  
 Tekom: BMNH 1973.2505 (not examined).

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## THE RELIABILITY OF THE TOE-CLIPPING METHOD WITH THE COMMON LIZARD (*LACERTA VIVIPARA*)

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### ABSTRACT

Out of a group of 954 individuals of *Lacerta vivipara* 8% showed naturally caused toe losses during a four year field study. Another 2% was naturally marked by nail losses or seriously damaged toes. The adult females had the greatest chance of natural toe loss, about three times as much as the adult males. For full reliability the toe-clipping method needs some additional data of the animals marked.

### INTRODUCTION

When studying lizards it is mostly necessary to be able to recognise the animals individually. During the last few decades a number of marking techniques have been developed which are used separately or in combination (e.g. Vogt, 1944; Carlström and Edelstam, 1946; Woodbury, 1956; Tinkle, 1967; Honegger, 1979). The most widespread marking method for lizards is toe clipping in certain combinations (Ferner, 1979).

The occurrence of natural toe loss, however, may cause confusion when identifying. Only a few field studies mention this problem (e.g. Tinkle, 1967; Schoener and Schoener, 1980). A population study on the common lizard (*Lacerta vivipara*) in the nature reserve 'Overasseltse en Haterse Vennen' near Nijmegen, in which a total of 954 animals were marked, offered the opportunity to test the reliability of the toe-clipping method.

### METHODS

The study area is formed by river dunes with some moorland pools. It is alternately covered by woods (coniferous as well as oak and birch coppice) and by

heathland and cultivated areas (Strijbosch, 1988). Within this study area four test sites were selected lying close to each other. They were visited each day and the lizards found were captured by hand, marked — if captured for the first time — and measured.

A maximum of one toe per foot was clipped. When reading the toes of each foot were numbered 1-5 from left to right as seen from dorsal. The combination of the toes clipped at the four feet — in the order left front, right front, left hind and right hind — gave the individual marking number. An unutilated foot had the figure 0. So an animal whose second toe of the left front foot was clipped as well as the third of its left hind foot and the fourth of its right hind foot bore the number 2034. This system offers the possibility to give 1,295 animals individual numbers (viz.  $6^4 = 1296$  minus one for the combination 0000).

Whenever we found an animal that had lost one or more toes through natural causes, this resulted in a 'natural' marking number or in an alteration of the number already given. Also when a nail was lost or when a toe was seriously damaged we gave the animal a new number in order to avoid confusion when reading. If an animal lacked more than one toe per foot we gave it a fraction number (e.g. number  $2\frac{3}{4}$  14 lacked an extra toe at the right front foot).

A correct identification of any animal was (sometimes considerably) supported by the data which we collected at each capture for the population study: date of capture, exact capture spot, age, sex, weight, snout-vent length, tail length, secondary tail growth if present, reproductive phase, sloughing phase, scars and other particulars if present.

## RESULTS

The occurrence of natural numbers or the alteration of clipped numbers were caused by toe and/or nail loss. Tables 1 and 2 give the numbers of these phenomena. Adult males and females were defined as those that were mature (i.e. in their third year and onwards). Subadults were animals in their second year and juveniles those born in the year of study. The numbers of the adult animals in the total period 1977-1980 were corrected for doubles, e.g. when an adult male was captured both in 1977 and 1978 it was counted as one individual for the period 1977-1980.

### TOE LOSS

From Table 1 it appears that most toe loss occurred in adult females (about 16% for the period 1977-1980); it was twice as much as for subadults (about 8%) and about three times as much as for adult males. So the adult females were the greatest risk-group. For the total group of animals identified (954 in the period 1977-1980) 8% of the number codes was caused by natural toe loss.

### TOE AND NAIL LOSS

Beside natural toe loss also serious damage to a toe and/or nail lead to an alteration of the marking number: it was then completely clipped resulting in a new number code.

Table 2 also shows that in general adult females had most toe and nail losses, one and a half times as much as subadults and about three times as much as adult males. The subadults lost the greatest number of nails. Within the total group over the period 1977-1980 some 10% of the animals had a natural marking number or a number altered through toe and/or nail loss.

If a distinction is made between different habitats within the study area (Strijbosch, 1988), it was remarkable that far more toe and nail losses were found in dry open habitats than in the moist, more closed one. This can be illustrated by the following figures, for which we counted all individual cases of toe or nail loss in the two different habitat types. In the open dry habitat we found 154 cases of natural mutilation in a total of 568 individuals, in the closed moist one 51 in 384 individuals. This difference was highly significant ( $\chi^2$ -test,  $P < 0.001$ ).

It was also investigated as to which toes were most vulnerable. We found that the front feet toes, all being more or less equal in length, had an equal chance of damage. The hind feet, however, have toes different in length: the fourth toe counting from the body is clearly longer than the other toes and it appeared to run the greatest risk of damage. For some investigators (e.g. Honegger, 1979) this is reason enough never to clip this fourth toe when marking lizards.

## DISCUSSION

Ferner (1979) mentions a number of criteria which must apply to an ideal mark or tag:

- it must not influence the survival chance or the behaviour of the animal.
- the animal must experience as little pain or stress as possible.

year	ad. ♂♂		ad. ♀♀		subad.		juv.		Total	
	A	B	A	B	A	B	A	B	A	B
1977	7	6.7	8	10.4	6	6.0	—		21	5.7
1978	3	4.2	14	16.3	9	8.8	—		26	6.7
1979	—		12	17.1	18	16.5	1	0.7	31	8.8
1980	1	4.0	2	9.5	1	2.1	3	3.6	7	3.9
'77-'80	11	5.8	31	16.5	30	8.4	4	0.9	76	8.0

TABLE 1: The number of individuals with natural toe loss (ad. = adult; subad. = subadults; juv. = juveniles; A = number; B = percentage of total number per age class).

year	ad. ♂♂		ad. ♀♀		subad.		juv.		Total	
	A	B	A	B	A	B	A	B	A	B
1977	7	6.7	9	11.7	8	8.0	—		24	6.4
1978	3	4.2	14	16.3	11	10.8	1	0.8	29	7.5
1979	1	2.9	14	20.0	26	23.8	2	1.5	43	12.2
1980	1	4.0	3	14.3	3	6.3	3	3.6	10	5.6
'77-'80	12	6.3	32	17.5	44	12.3	6	1.4	94	9.9

TABLE 2: The number of individuals with toe and nail loss (for legends see Table 1).

- the animal must be recognised later individually.
- the marking must be permanent.
- it must be easily read or seen.
- it must be applicable to animals of different sizes.
- it must be suitable both in the laboratory and in the field and the materials used must be cheap.

The toe-clipping method meets these demands more or less. Woodbury (1956) does mention the possibility that the clipping of toes might harm the lizards but Ferner (1979) did not find any indication or proof of that. The frequent capture of the animals in itself, however, may influence the survival chances or the behaviour of the animals (Bauwens, 1985). As for the permanent character of toe mutilation it may be said that regeneration of toes once lost has never been found (Bellairs, 1969).

An ideal mark should also meet the condition that it cannot be altered without knowledge of the investigator. The toe-clipping method does not always meet this demand. From this study it appeared that some 10% of the animals bore a marking number which was naturally caused or which was altered through natural toe and/or nail loss in the course of time. A six-year population study of *Uta stansburiana* showed 3% natural marking numbers (through toe loss), viz. 100 out of 3,500 numbers (Tinkle, 1967). In that species the adult males appeared to be most vulnerable, three times as much as the adult females. This lower probability of toe loss in *Uta stansburiana* will be particularly influenced by its relatively short life span (1-2 years) as compared to that of *Lacerta vivipara* (up to 7 or 8 years for females). According to Tinkle (1967) this toe loss has never led to serious problems with the identification of the animals.

Although 10% unreliability for *Lacerta vivipara* seems rather high, the field work proved that the chance of confusion is nevertheless slight. To avoid this confusion, however, the animals must be caught

frequently and a great number of individual characteristics must be recorded. The more reference data of the animal are available the less one depends on the unreliability of the marking number. Certainly when a population study does not meet the above demands, natural toe loss, which inevitably occurs, prevents a complete reliability of the toe-clipping method.

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## POPULATION ECOLOGY AND CONSERVATION OF TORTOISES: THE EFFECTS OF DISTURBANCE

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### ABSTRACT

Population characteristics of sympatric *Testudo hermanni* and *T. graeca* were compared at four sites in northern Greece; Alyki, Epanomi, Keramoti and Lagos. These had different habitats and levels of human disturbance. The density of tortoises larger than 10cm was similar at all sites, in the range 7-21ha<sup>-1</sup>. Population size structures were more variable. The ratio of juveniles to adult females ranged from about 0.1 at the most disturbed site (Lagos) to about 4 in a protected area (Epanomi). This ratio was similar for the two species at any site, even though they occupied different habitats. The main feature of disturbance was thought to be predation of eggs and juveniles by human commensals (rats and domestic animals) rather than habitat degradation.

The sample sex ratio of *T. hermanni* was male-biased at all four sites, with an average of 3.1 males per female. Males had more tick parasites than females, higher body temperatures, and were recaptured twice as frequently. There was an even sex ratio in *T. graeca*, the sexes had similar numbers of ticks and body temperatures, and females were recaptured more frequently. The population sex ratio of *T. hermanni* is known to be male-biased at Alyki. The data on ticks, body temperatures, and recapture frequencies show that sample sex ratios are complicated by sexual differences of activity or microhabitat use. It is suggested that male *T. hermanni* used more open areas than females, within the wood, scrub or heath occupied by this species. *T. graeca* occupied coastal heath at all sites, an open habitat with little spatial variation of cover.

### INTRODUCTION

Although tortoises may be found in many habitats in the Mediterranean region, most populations survive at low density. High population densities are often found, however, in coastal areas where farming is unproductive, and which have therefore remained undisturbed. These areas are now under threat from development for tourism (Honegger, 1981). This paper describes the tortoise populations at four coastal sites in north-eastern Greece, which were examined during a study of the habitat separation of *T. hermanni* and *T. graeca* (Wright, Steer and Hailey, submitted). The main reason for the choice of sites was the presence of both tortoise species and a range of habitat types. However, the sites also suffered from different degrees of disturbance, and so made possible a comparative study of the effect of disturbance on tortoise populations.

### METHODS

#### SAMPLING METHODS

Tortoises were studied at the four sites Alyki, Epanomi, Keramoti and Lagos (Fig. 1) in July and August 1985. A large-scale vegetation map of each site was made using landmarks and a measuring line. Five observers were used for 7-10 days at each site, in addition to the vegetation survey. They sampled the area along straight transects so that the whole area was covered roughly uniformly. Distances of sightings

perpendicular to the transect were used to calculate population density (Hailey, 1988). Tortoises were handled and individually marked by notching marginal scutes as described by Stubbs, Hailey, Pulford and Tyler (1984), and an independent estimate of population density was obtained using the Jolly mark-recapture method (Begon, 1979). Body temperatures of animals larger than about 10cm were measured rectally with a mercury thermometer.

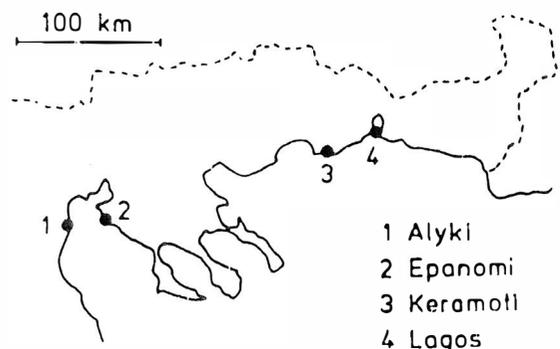


Fig. 1 Location of the four sites in north-eastern Greece.

Tortoises of less than 10cm (*T. hermanni*) or 12cm (*T. graeca*) straight carapace length (SCL) could not be sexed by external characters, and are termed juveniles. The SCL at maturity is considered to be 14cm in males (both species) and 15cm (*T. hermanni*) or 16cm (*T. graeca*) in females; tortoises of intermediate size are

termed subadults. The number of tick parasites on exposed areas of skin was counted. This excluded any ticks hidden behind the legs or on the neck, as these parts could not be exposed easily.

#### SITE DESCRIPTIONS

Brief descriptions of the sites are given below. Maps and details of the vegetation types are given by Stubbs, Swingland, Hailey and Pulford (1985) for Alyki, and by Wright *et al.* (submitted) for Epanomi, Keramoti and Lagos.

#### Alyki

A strip of heathland separating a shallow lagoon and salt works from the sea. The results reported here were from sector 13, the southern heath; this sector has not been described in previous papers on Alyki, and so a map is provided in Fig. 2. This sector was badly damaged by fire and plough in 1980 (Stubbs, Hailey, Tyler and Pulford, 1981) but the vegetation had largely regenerated by 1985, except for the large shrubs.

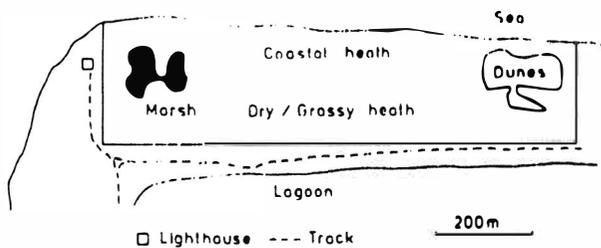


Fig. 2 A map of Alyki sector 13, the southern heath.

#### Epanomi

A headland of dunes and coastal heath around a lagoon. The study area was next to a holiday village and a large camping ground, 10km south-west of Epanomi town. Three areas were defined (Wright *et al.*, submitted), but few tortoises were found in area 3, which is not considered in this paper:

1. A rectangle of heath vegetation structurally intermediate between dry heath and coastal heath.
2. An area of coastal heath on loose sand and dunes.

#### Keramoti

The main site was along the coast east from the small town and port; two areas were defined:

1. A strip of dunes and coastal heath behind the beach.
2. A large area with belts of broadleaf woodland in open grazed grassland on sandy soil. The woodland had thick ground vegetation and shrub layers.

Another site (Area 3) is also considered in this paper. This was a small island west of the town, reached by a small bridge, and included coastal heath, scrub and mixed woodland. This was studied as an example of a small tortoise population living at high density in a small well-defined area.

#### Lagos

The site was on a spit of land between the sea and lake Vistonika, west of the town and port of Lagos.

Three areas were defined (Wright *et al.*, submitted) but area 3 is not considered in this paper as few tortoises were found there.

1. A plantation of shore pine with scrub along its coastal and roadside edges. There was little ground vegetation. This area was frequently used for camping and picnics.

2. An area of coastal heath next to the pine wood, including some grazed grassland and a line of dunes along the sea.

#### METHOD OF ANALYSIS

The method for the estimation of population density (Hailey, 1988) was developed to take account of the low activity of tortoises, by calibrating a standard transect sampling method in areas of known population density. This enabled the proportion of the population which are available for finding (PAF) at the time of sampling to be calculated. At times of peak daily activity in summer, PAF was calculated to be 0.15 and 0.10 in male and female *T. hermanni* of SCL 10cm or more, respectively. This value was based on surveys of three populations of *T. hermanni* in 1981-1983.

The activity of tortoises in Greece during the summer of 1985 was low compared to other years, probably because this was an unusually dry year (M. Lazaridou-Dimitriadis and R. E. Willemsen, pers. comm.). A calibration was made in July and August 1985 in a population of known density (Alyki main heath), simultaneously with the surveys of the other sites. The results of 256 sightings of *T. hermanni* enabled calculation of PAF as:

Morning: males, 0.040      females, 0.047  
Evening: males, 0.048      females, 0.024

There was thus less difference between the sexes in 1985, as well as lower activity generally, than in 1981-1983. In this paper sightings of males and females were pooled, and sighting frequency was averaged over morning and evening activity periods. This gave a single density estimate for all individuals larger than 10cm, using the average value PAF = 0.04. In the absence of specific data, this value was also used for *T. graeca*.

Statistical tests follow Sokal and Rohlf (1981); results in tables are shown as NS =  $P > 0.05$ , \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ .

## RESULTS

#### POPULATION DENSITY

Sighting frequency, effective transect width and the calculated population densities of tortoises larger than 10cm are shown in Table 1, together with estimates from mark-recapture. It was not possible to use the transect method in the strips of dense woodland of Keramoti area 2. Recapture frequencies were too low to give accurate estimates from mark-recapture, as shown by the large standard errors. Indeed, the population sizes estimated by mark-recapture were lower than the number of individuals marked in six of

Site/area	(ha)	Species	W (m)	N	F (No.h <sup>-1</sup> )	Density (No.ha <sup>-1</sup> )	Individuals marked	Jolly No. (and S.E.)
Alyki 13	12	<i>T.h.</i>	4.4	201	2.0	19	162	260 (235)
Epanomi 1	18	<i>T.h.</i>	4.8	36	1.2	10	32	15 (12)
1	18	<i>T.g.</i>	6.5	63	2.6	16	61	53 (50)
2*	10	<i>T.g.</i>	4.9	29	1.5	19	28	0 (0)
Keramoti 1	19	<i>T.g.</i>	8.1	68	1.8	9	44	16 (15)
3	4	<i>T.g.</i>	4.8	43	2.4	21	30	14 (6)
Lagos 1	6	<i>T.h.</i>	4.1	78	1.0	10	63	39 (33)
2	6	<i>T.g.</i>	7.3	93	1.3	7	67	84 (74)

TABLE 1: Sighting characteristics and density estimates for *T. hermanni* and *T. graeca* larger than 10cm. The effective transect width W (based on N sightings) and mean sighting frequency (F) at peak activity times are defined by Hailey (1988); density is calculated using equation (2) in that paper, using PAF = 0.04. The number of individuals marked, and the Jolly mark-recapture estimate (with S.E.) is also shown. \* Walking speed 2km.h<sup>-1</sup>, otherwise 3km.h<sup>-1</sup>.

the eight populations. In the other two populations, the estimated population size was equivalent to a density similar to that calculated from transect sampling (Table 1). The inadequacy of short-term mark-recapture studies for estimating tortoise population density has been noted previously (Hailey, 1988), and will not be discussed further.

#### POPULATION STRUCTURE

This paper uses the sample structure of individuals (that is, excluding recaptures) as an estimate of the population structure. It should be noted that this underestimates the proportion of smaller tortoises, which are harder to find (see sighting profiles in Hailey, 1988). The bias against small animals decreases as the sample approaches a complete census. Sample structure provides a useful comparison between sites which are sampled at a similar intensity, as shown by the ratio of sightings to individuals marked (Table 2).

Only five *T. graeca* were found at Alyki during the survey of sector 13 in 1985. We therefore include data on population structure collected over the whole Alyki area between 1980 and 1986, using the size of each tortoise when last captured. The number of individual juveniles and adult males and females marked at each site is shown in Table 3a.

#### Sex ratio

The sex ratio is described as the number of adult males per adult female. This ratio differed significantly from 1:1 in *T. hermanni* at all four sites, with a mean of 3.1 males per female (Table 3b). There was also significant variation of the sex ratio between sites. In contrast the overall ratio was 1.1 males per female in *T. graeca*, not significantly different from 1:1, and there were no significant differences between sites.

#### Size structure

The size frequency distributions of individuals are shown in Figs. 3 (*T. hermanni*) and 4 (*T. graeca*). Juveniles have been divided evenly between the sexes. There were large differences in size structure between the four sites, with many small individuals at Epanomi, and few at Lagos. The trend was similar for both species.

We use the ratio of juveniles: adult females as a summary statistic of the size structure of tortoise

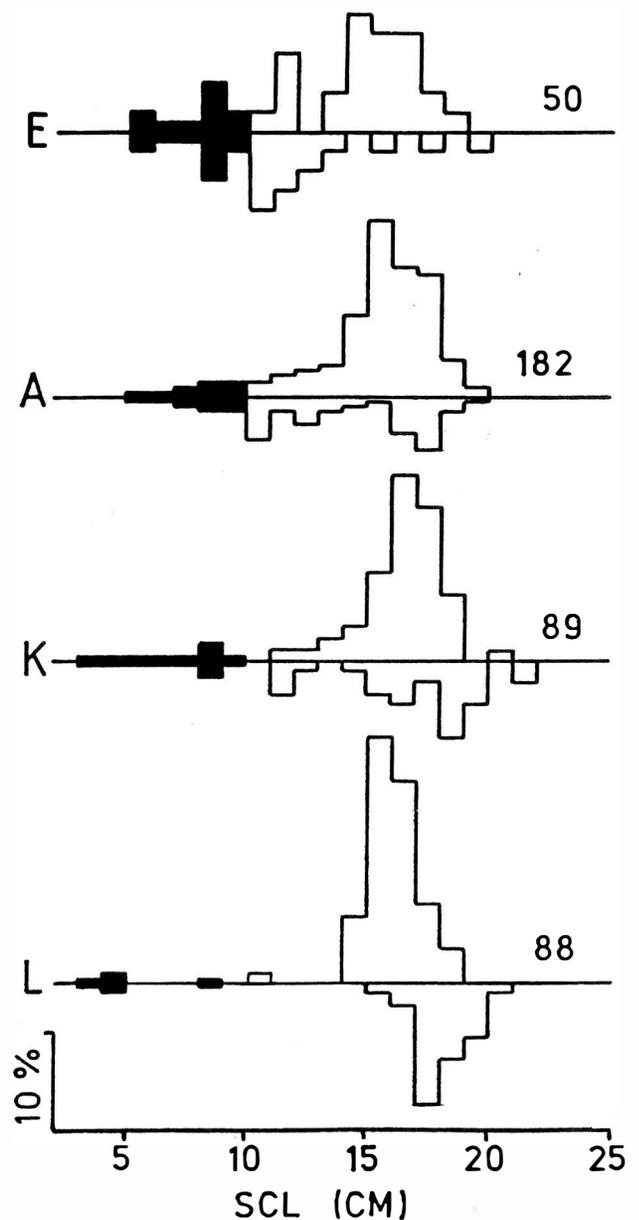


Fig. 3 Size frequency histograms of *T. hermanni* at Epanomi (E), Alyki (A), Keramoti (K) and Lagos (L), excluding recaptures. Males are shown above the line, females below; juveniles less than 10cm are divided evenly between the two sides of the histogram (shaded). Percentages are of the total number of individuals, which is also shown.

Site	Recaptures	All adults		Adult male <i>T. hermanni</i>		
		Individuals	Ratio	Recaptures	Individuals	Ratio
Alyki	32	126	0.25	28	104	0.27
Epanomi	14	53	0.26	6	19	0.32
Keramoti	47	144	0.33	17	49	0.35
Lagos	46	173	0.27	18	56	0.32
G test		1.15 NS			0.58 NS	

TABLE 2: The ratio of recaptures to individuals marked of all adult tortoises, and of adult male *T. hermanni*, to show that sampling intensity was similar at the four sites.

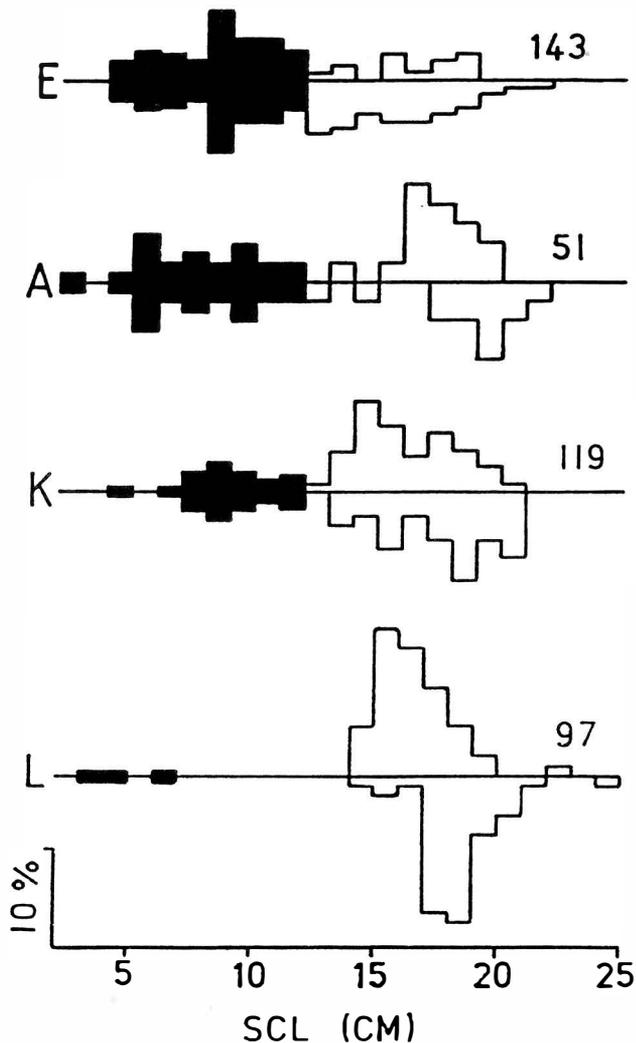


Fig. 4 Size frequency histograms of *T. graeca*. Explanation as in Fig. 3, except that juveniles are less than 12cm.

populations, for use in conservation. This excludes males for two reasons. First, the sex ratio varies considerably between sites and in different species (above). Second, tortoises are promiscuous (Swingland and Stubbs, 1985), so a population's reproductive potential is not directly related to the number of males.

Values of this ratio are shown in Table 3c. There were large and significant differences between the sites, ranging from about 0.1 at Lagos to about 4 at Epanomi. A similar trend was shown by the two species; ratios did not differ significantly between them at any of the four sites.

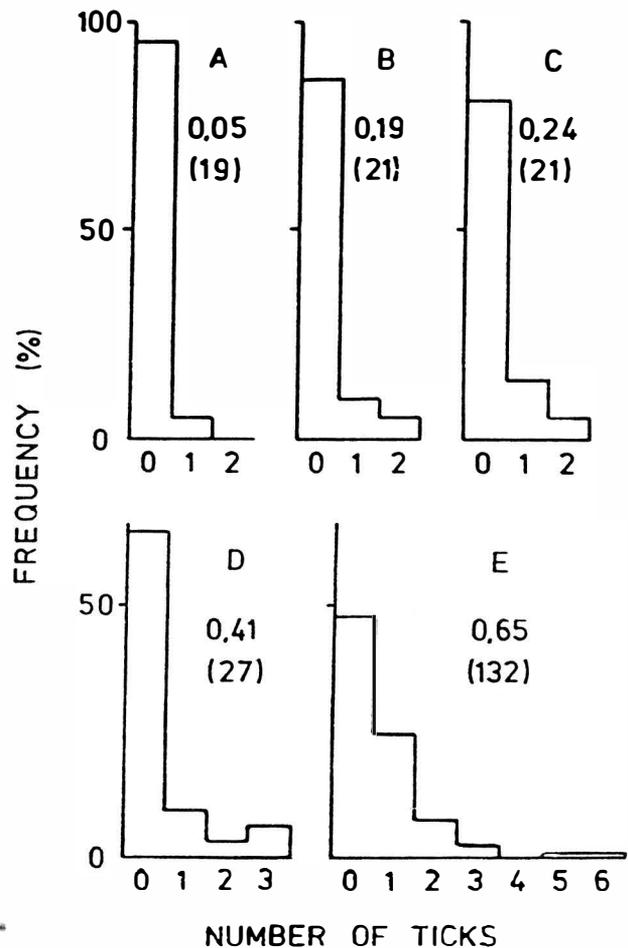


Fig. 5 Frequency histograms of numbers of ticks per tortoise in *T. hermanni* at Alyki. (a) juveniles, (b) subadult females, (c) subadult males, (d) adult females, (e) adult males. The mean and sample size are shown.

TICK INFECTIONS

The ticks infecting *T. hermanni* at Alyki in 1979 were identified as *Hyalomma aegyptium* (Stubbs, Espin and Mather, 1979), which is a common parasite of tortoises (Reichenbach-Klinke and Elkan, 1965; Frank, 1981). Ticks on tortoises at Alyki in subsequent years, and at other sites, were apparently the same, but have not been reliably identified.

Juvenile and subadult tortoises had fewer ticks than adults in each species and at each site. The data for *T. hermanni* at Alyki are shown in Fig. 5 as an example; similar patterns were shown in other samples where the number of small tortoises handled was sufficiently

Site	<i>T. hermanni</i>			<i>T. graeca</i>		
	Males	Females	Juveniles	Males	Females	Juveniles
Alyki	104	22	17	15	11	22
Epanomi	19	3	11	12	19	83
Keramoti	49	22	9	39	34	26
Lagos	56	26	3	49	42	3

(a) Sample sizes. Data for *T. graeca* at Alyki include captures 1980-1986.

Site	Males/Females	$\chi^2$	Males/Females	$\chi^2$
Alyki	4.7	53.4 ***	1.4	0.61 NS
Epanomi	6.3	11.6 ***	0.63	1.58 NS
Keramoti	2.2	10.3 **	1.1	0.34 NS
Lagos	2.1	11.0 ***	1.2	0.54 NS
G test	8.76*		2.69 NS	
Pooled	3.1	79.8 ***	1.1	0.37 NS

(b) Ratio of adult males per adult female at each site, and at all sites pooled. The  $\chi^2$  tests are against an expected 1:1 ratio; the G test is of variation of the ratio between sites.

Site	Juveniles/Females	Juveniles/Females	G
Alyki	0.77	2.0	3.80 NS
Epanomi	3.7	4.4	0.06 NS
Keramoti	0.41	0.76	1.77 NS
Lagos	0.15	0.07	0.29 NS
G test	21.6***	84.1***	

(c) Ratio of juveniles per adult female at each site. G tests comparing the two species at each site, and the four sites for each species.

TABLE 3: Population structure in terms of sex ratio and ratio of juveniles to adult females.

Site	Alyki	Keramoti	Lagos	Epanomi
<i>T. hermanni</i>	0.61 (159)	0.67 (92)	1.44 (81)	2.00 (29)
<i>T. graeca</i>	2.64 (31)*	2.40 (141)	2.12 (109)	3.46 (46)

(a) All adult tortoises.

Male	0.65 (132)	0.76 (67)	1.69 (55)	2.04 (24)
Female	0.41 (27)	0.44 (25)	0.92 (26)	1.80 (5)
Male/Female	1.58	1.73	1.84	1.13

(b) Sexual differences in *T. hermanni*.

Male	2.53 (15)	2.59 (66)	2.06 (49)	3.80 (15)
Female	2.75 (16)	2.23 (75)	2.17 (60)	3.29 (31)
Male/Female	0.92	1.16	0.95	1.15

(c) Sexual differences in *T. graeca*.

TABLE 4: Mean infection levels with the tick *Hyalomma aegyptium* at the four sites. Values are the mean number of ticks per adult tortoise (with number of tortoises), including recaptures but excluding tortoises with numerous juvenile ticks (see Fig. 6). \*Results from July or August 1980-1986.

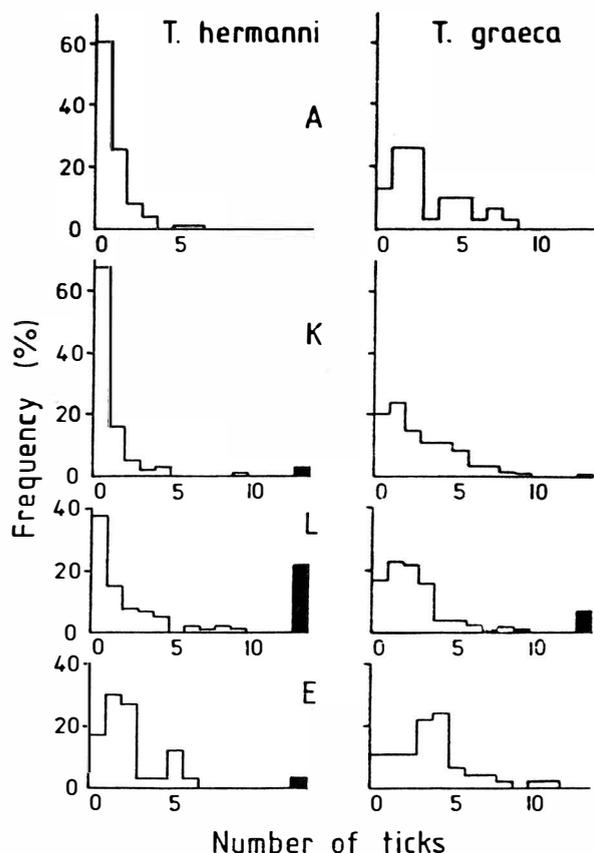


Fig. 6 Frequency histograms of ticks per tortoise at Alyki (A), Keramoti (K), Lagos (L) and Epanomi (E). Adult tortoises only, sexes pooled. The shaded bars show tortoises with 15-60 juvenile ticks. Means and sample sizes in Table 4.

large. The subsequent analysis considers ticks on adult males and females only.

Mean infection levels on *T. graeca* varied from 2.1 to 3.5 at the four sites. *Testudo hermanni* had fewer ticks, and there was more variation between sites, with means from 0.6 to 2.0 (Fig. 6). Adult male *T. hermanni* had more ticks than females, whereas male and female *T. graeca* had similar infection levels (Table 4).

	<i>T. hermanni</i>	<i>T. graeca</i>
Male	29.0 ± 3.2 (284)	30.3 ± 2.9 (116)
Female	28.0 ± 3.1 (81)	30.8 ± 3.1 (143)
t test	2.53*	1.45 NS

(a) Mean body temperature ± S.D. (with sample size).

	Individuals	Ratio	Individuals	Ratio
Male	69 : 228	0.30	19 : 100	0.19
Female	11 : 73	0.15	40 : 95	0.42
G test	4.36*		6.70**	

(b) Number of recaptures : individuals, and ratio.

TABLE 5: Sexual differences of (a) body temperature and (b) recapture frequency in adult *T. hermanni* and *T. graeca*, all sites pooled. t and G tests are between the sexes. Keramoti area 3 included in (a) but not in (b).

BODY TEMPERATURE AND ACTIVITY

Activity periods and body temperatures of *T. hermanni* and *T. graeca* at the four sites have been compared by Wright *et al.* (submitted) in relation to habitat use. That paper pooled all measured body temperatures, that is from all tortoises larger than about 10cm, irrespective of sex. Sexual differences of body temperature are analysed here, in relation to interspecific differences in sex ratio and tick infection. Adult male *T. hermanni* had significantly higher body temperatures than adult females (Table 5), by an average of 1.0°C. There was an opposite trend in *T. graeca*, females having body temperatures about 0.5°C higher, but this was not significant.

There were significant differences between the probability of recapture of males and females in both species (Table 5). Male *T. hermanni* were recaptured twice as frequently as females, while exactly the opposite was found in *T. graeca*.

HABITAT DISTURBANCE

There was no evidence of recent catastrophic events at any of the sites. There was presumably some disturbance when the plantation of shore pine was initiated at Lagos. This was thought to be about 30 years ago, from the size of the trees. All of the sites were currently liable to some degree of chronic disturbance.

There was little direct disturbance at Epanomi, where camping was restricted to a fenced area; most of the site was a protected area. Alyki was also undisturbed, because of its isolation: this area is recognised as being of national interest, but is without effective protection. There was some beach activity and fishing at both Epanomi and Alyki, but vehicles kept to definite tracks. Camping at Keramoti was less regulated, and there was more use by vehicles as the area was close to the town. The site at Lagos was also close to the town, and used intensively for unofficial camping and for day trips: there were abundant traces of human activity (litter, faeces).

The use of the sites by grazing animals varied seasonally. For example at Alyki sheep used the heath from October to May, and were moved to farms several km away for the summer. Epanomi was also visited at different times, and sheep were seen in winter and spring, but not in summer. Sheep were seen in summer at Keramoti and at Lagos.

THE ISLAND POPULATION

The island (area 3) at Keramoti had a range of habitat types similar to those found in other areas at that site. Body temperatures were therefore pooled with those in areas 1 and 2, and will not be considered separately. Population density of *T. graeca* larger than 10cm in the 4ha island was estimated as 21ha<sup>-1</sup>, the highest of any area (Table 1). In total, 33 *T. graeca* were marked in area 3, comprising 8 juveniles, 5 sub-adults, 10 adult females, and 10 adult males. The sex ratio (1:1) and juvenile to female ratio (0.8) were thus similar to those of *T. graeca* in areas 1 and 2 (Table 3). Three adult *T. hermanni* were also found.

## DISCUSSION

## SAMPLING AND SIZE STRUCTURE

Juveniles are often under represented in studies of tortoises (e.g. Lambert, 1982; Meek and Inskip, 1981; Meek, 1985). This pattern has implications for dynamics and conservation, if it reflects the true population structure rather than the difficulty of finding juveniles (Lambert, 1981). For example, Stubbs and Swingland (1985) found fewer juvenile *T. hermanni* in woodland in France than in heathland in Greece, but could not rule out the possibility that juveniles were simply harder to find in woodland.

The present study comparing two species in several habitat types at four sites is therefore interesting in two respects:

1. *Testudo graeca* occupied similar coastal heath habitat at all four sites (Wright *et al.*, submitted). The substantial variation of size structure between sites therefore reflects differences in their true population structures.

2. The size structures of the two species were similar at each site, even though *T. hermanni* occupied habitats ranging from grassy heath to pine and broadleaved woods. This suggests that habitat type has a rather small effect on the difficulty of finding juveniles, and that the population size structures of the two species are determined by similar factors.

## EFFECTS OF DISTURBANCE

The four sites were found to have densities of tortoises larger than 10cm of 7 to 21ha<sup>-1</sup>. These coastal sites thus support dense populations compared to inland thorn scrub habitat, where sightings are often an order of magnitude less frequent (Lambert, 1981; personal observations). However, adults of long-lived species may persist for several years after recruitment has ended (e.g. Berry, 1976; Beebe, 1979). In addition, large, old female *Testudo* may have reduced reproductive potential (Hailey and Loumbourdis, 1988). The population density of adults is therefore not sufficient information to assess the need for active conservation measures.

The ratio of juveniles to adult females must also be considered. This varied widely between the sites, and was probably related to disturbance. Juvenile tortoises and nests are vulnerable to predation by human commensals such as rats, cats and dogs, which are more abundant near towns. The site at Lagos was the nearest to a town, followed by Keramoti; Epanomi and Alyki were relatively isolated.

## CONSERVATION TECHNIQUES

This section discusses ecological techniques for conserving tortoise populations, rather than general policies for tortoise and habitat conservation.

The scarcity of juveniles at Lagos was similar to that in woodland in France (Stubbs and Swingland, 1985), but the causes were probably different. The problem in France was deterioration of the habitat; open areas used for nesting were becoming overgrown following the decline of traditional agricultural practices. Nests were then concentrated in a few remaining open areas, where they were vulnerable to natural egg predators

such as beech marten and badgers (Stubbs and Swingland, 1985). It is undesirable to control such natural predators, and so indirect conservation measures must be used, such as:

1. Habitat modification, to prevent encroachment on open areas (e.g. Corbett and Tamarind, 1979).

2. Removal of eggs and hatching in captivity, dispersing the juveniles to avoid concentrations of predators (Devaux, Pouvreau and Stubbs, 1986).

The problem of human commensals at sites such as Lagos needs different solutions. It would be possible to control these directly, by fencing out cats and dogs and trapping rats. A more economical measure would be the removal of eggs and releasing juveniles, as in France. The juveniles should, however, be kept in captivity for a few years before release so that they are large enough to resist predators, rather than simply dispersing them to avoid concentrations of predators.

## SEX RATIO, ACTIVITY AND TICK INFECTIONS

Sample sex ratios of adult *T. hermanni* were biased towards males at all four sites. Was this because males were more abundant than females, or because they were more available for finding? These explanations are not exclusive, and both are known to contribute to the male bias at Alyki (Hailey, 1988). The main difference between the behaviour of male and female tortoises is that males must search for mates. This behaviour could increase the availability for finding of males in two ways; 1. Males are more active. 2. Males frequent places where tortoises are more obvious, such as open microhabitat.

The even ratio in *T. graeca* suggests that males are not more active than females in this species. This conclusion should apply to *T. hermanni*, as active searching for mates is similar in the two species, although the details of courtship behaviour differ. We therefore favour hypothesis 2: male *T. hermanni* are more available for finding than females because they frequent more open areas. This would not affect the sex ratio of *T. graeca*, as this species occupied open coastal heathland where there was little variation of cover. Sighting profiles of male and female *T. hermanni* are similar (Hailey, 1988), because tortoises moving in cover are rarely found, and so do not skew the profile towards short distances from the transect. Male *T. hermanni* had higher body temperatures than females, consistent with their use of more open areas.

Infection of tortoises by ticks is from unattached ticks in the environment, rather than between tortoises, and will be related to the behaviour of both ticks and tortoises. The sexes had similar infection levels in *T. graeca*, consistent with similar activity levels within a uniform habitat. *Testudo graeca* had more ticks than *T. hermanni*, suggesting that transmission was greater in open habitats. This could be explained by the observed tendency for free infective ticks to climb. Ticks would be concentrated into the few plants in open areas, which would bring them into contact with feeding tortoises, increasing the chance of infection. Male *T. hermanni* had more ticks than females, consistent with the suggested use of more open microhabitat.

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## FUNCTIONS OF THE FOAM IN THE FOAM-NESTING LEPTODACTYLID *PHYSALAEEMUS PUSTULOSUS*

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### ABSTRACT

The possible functions of floating foam nests in frogs of the family Leptodactylidae were investigated using the common neotropical species *Physalaemus pustulosus* as an example. The results showed that:

1. The foam serves little thermal function, with foam and water temperatures being very similar, and time to hatching in foam compared to water also being similar.
2. The foam has some limited ability to protect eggs and hatchlings from desiccation.
3. Tadpoles of another species attacked intact foam nests, and isolated eggs were palatable to aquatic insect larvae and other tadpole species.

These results are discussed in the context of reproductive mode evolution, and other possible functions of foam — aeration and nutrition — are considered.

### INTRODUCTION

It is well known that a common feature of the anuran family Leptodactylidae is the deposition of eggs in a mass of foam, either on the surface of water, or in a burrow. As Martin (1967, 1969) and Heyer (1969) have suggested, the family appears to show an evolutionary shift away from reproduction in water to an increasingly terrestrial mode, culminating in species with larvae that do not feed and are entirely terrestrial. However, the function of the foam, in the presumably primitive species which deposit foam nests in water, often along with other anuran species that show more conventional breeding modes, is not clear. In the literature, floating foam nests have three suggested functions: 1. reduction of predation, 2. prevention of desiccation, and 3. alteration of egg temperatures. These suggestions seem rarely to have been tested, except for temperature where the two published studies given contradictory results.

Using the widely distributed neotropical leptodactylid *Physalaemus pustulosus*, the present study assesses these three possible functions of foam, and speculates on some others.

*Physalaemus pustulosus* (= *Engystomops*; = *Eupemphix*, Lynch, 1970) is found in Central America, the northern part of South America, and in Trinidad — where my observations were made. In Trinidad, *P. pustulosus* is most abundant at the low altitudes of the Caroni plain, but is also found high in the Northern Range mountains, for example at over 600m in the Arima valley. The frog breeds throughout the rainy season, and following wet nights, its foam nests can be found attached to emergent vegetation at the margins of garden ponds, tyre ruts, flooded grassland or wasteground and even slow-moving drainage ditches (Fig. 1). Nests are made both in shade and in the open, with no obvious preference. The bodies of water used

for breeding by *P. pustulosus* are used by many other Trinidadian anurans, but generally lack fish. Each nest contains a few hundred eggs, and tadpoles hatch from the foam 2-3 days after nest deposition. *P. pustulosus* tadpoles are cryptically patterned, bottom-living and not well adapted to life in flowing water. In Panama, *P. pustulosus* is called the tungara frog; in Trinidad, the punglata or pungrara frog (Ryan, 1985; John Seyjagat, personal communication), all names being based on the sound of the call.



Fig. 1 *Physalaemus pustulosus* nests in typical habitat — a flooded piece of waste ground. Three white foam nests are seen floating at the surface of a shallow pool, amongst vegetation.

### MATERIALS AND METHODS

#### COLLECTION AND NESTS

The foam nests used in this study were found in temporary pools and drainage ditches near the University of West Indies campus at St. Augustine, on the Caroni plain in Trinidad, during July 1987. Freshly-made nests were collected early in the morning

after wet nights. A few eggs were routinely removed for staging to ensure nests were fresh. All eggs tested were gastrulas at the time of collection.

#### TEMPERATURE MEASUREMENTS AND HATCHING TIME

Five freshly-made nests were placed individually in 2 litre size polythene tubs, and floated on the surface of water at a depth of 18mm. To check on the minimum time to hatching, and on possible effects of high temperatures, 6 eggs were isolated from each nest and floated, essentially foam-free, on the surface of water in a beaker placed in each tub. Two tubs were placed outdoors in the open, two outdoors in shade, and one in the laboratory. The temperatures of water in each tub, air at 5cm above the water surface, the foam surface and foam mass centre were measured at regular intervals over the next 2 days, using an LDC digital thermometer with external sensing probe. Late in incubation, the foam collapsed to a smaller volume and became crusty at the surface if kept dry; when this happened only a single foam temperature measurement could be made. Along with temperature measurements, larval hatching time and the weather were monitored.

#### FOAM NEST DESICCATION AND FOAM COLLAPSE

Nine freshly-made foam nests were placed in 2 litre size polythene tubs, with the foam resting on four layers of damp tissue. Several eggs from each nest were isolated and either floated on the surface of water in a beaker to check hatching time, or placed individually on the surface of the damp tissue beside the foam nest. Nests were then left in the laboratory, either with the

tub lid on (6 nests) or with no lid (3 nests). Four more nests were set up, in tubs with no lids, using a layer of damp mud instead of tissue. Egg development was monitored as detailed in the Results section.

To test what happens to the water in the foam, late in incubation, when the foam collapses, four fresh nests were weighed, then incubated floating on water in individual tubs for 48h (when all hatchlings had left the foam) either with the lid on or off. The remaining foam and the total clutch of hatchlings were then weighed.

#### OBSERVATIONS ON FOAM NEST PREDATION

Observations on tadpoles of *Leptodactylus fuscus* attacking complete foam nests were made both in the field and in the laboratory. Since it was unclear whether the tadpoles were feeding on both foam and eggs, eggs were isolated from the foam and placed in tubs for 24h with potential predators — as well as *L. fuscus* tadpoles, odonate nymphs and large tadpoles of *Bufo marinus* and *P. pustulosus*, all collected in the St. Augustine area. Eggs were left floating on the surface of water with a bubble of foam attached, or were sunk.

## RESULTS

#### TEMPERATURE MEASUREMENTS AND HATCHING TIME

Fig. 2 shows the temperature records of the 5 foam nests monitored, as well as the weather during the observation period. Table 1 shows the timetable of hatching of tadpoles from these 5 foam nests.

Nest Number and Location		Time (h)					
		37	41	45	56	63	69
LABORATORY	Nest Beaker		2 6/6	20	200	7 no more in foam	
OPEN 1	Nest Beaker	20	40 1/6	50 4/6	200 6/6	100 a few still in foam	All out of foam
OPEN 2	Nest Beaker	5	40 1/6	60 4/6	200 6/6	5 a few still in foam	10 All out of foam
SHADE 1	Nest Beaker			20 3/6	30 6/6	200 some still in foam	250 a few still in foam
SHADE 2	Nest Beaker			2/6	30 5/6*	25 many still in foam	200 a few still in foam

TABLE 1: Hatching timetable for foam nests whose temperature changes are recorded in Fig. 2.

The time axis assumes for convenience that nests were made at the middle of the night before they were collected and counts that time as 0h. For foam nests, numbers of hatchlings found in the tubs at each time are recorded. At 56h, foam masses were removed from original tubs so as to obtain an accurate estimate of numbers still to leave the foam. Numbers recorded for 63h and 69h are therefore tadpoles that emerged *after* 56h. Numbers hatching in beakers are given as the proportion out of the original 6 until all are hatched. \* = one egg died.

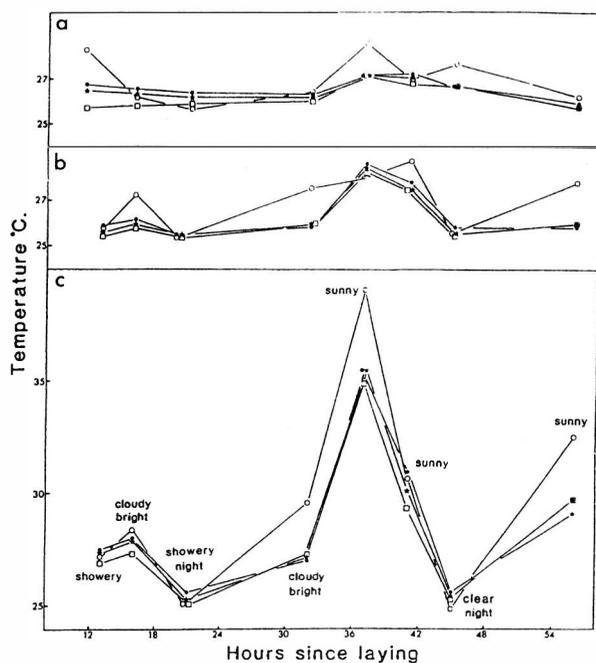


Fig. 2 Temperature records of foam nests. Time is measured since time of laying, assumed as middle of night before nest collection, (a) nest kept in the laboratory, (b) nests in shade outside; each temperature record is the mean of two nests, (c) nests in open outside; each temperature record is the mean of two nests.

Symbols: o = air temperature; ● = water; ★ = foam surface; □ = foam centre. Notes on weather at times of recording are given on c.

The results show the following:

1. Air temperature was consistently higher than foam or water.
2. Water temperature was consistently above deep foam, which was usually above foam surface temperature. The differences were small, generally less than 1°C separating all three. The only time when foam temperature was above water was on the final morning, when foam structure had collapsed.
3. In the open, temperature fluctuated considerably, influenced by solar radiation, while in the shade outside and in the laboratory, there was a gentle daily cycle.

4. Hatching time was influenced by temperature. Hatching occurred considerably earlier in the two open outside tubs than in the shaded ones. But short bursts of high temperature are less important than the overall level. Although foam temperature briefly reached 35°C outside in the open, most of the incubation period was spent between 25 and 27°C, not dissimilar to the other tubs. Hatching in the laboratory was not much later than outside in the open, laboratory temperatures being a little above those outside in the shade.
5. There was no evidence for thermal damage to the eggs. Eggs in foam and eggs floating at the water surface without foam outside in the open both exceeded 35°C for a time, and hatched as normal embryos.

#### FOAM NEST DESICCATION AND FOAM COLLAPSE

For the 6 nests incubated on the surface of moist tissue in tubs with the lid on, results were consistent. Isolated eggs on the tissue surface failed to hatch, though they did develop to some extent. The vast majority of eggs in the foam developed and hatched normally. However, this was because these eggs were not subjected to desiccation. With the tub lid on, the foam surface remained moist through a 3 days incubation period. In addition, after about 2 days incubation, the foam structure collapsed, releasing water into the bottom of the tubs: this water was adequate to maintain the tadpoles for the 3 days of the experiment.

In the case of the 3 nests incubated on the surface of moist tissue in tubs with the lid off, the foam surface became dry and crusty after only 1 day and eggs near the foam surface died. When water was added after up to 2 days (2 nests), the majority of tadpoles survived and soon emerged from the foam into the water. But if water was added after 3 days (1 nest), the foam was very dry and there were no survivors. Similarly, there were no survivors after 3 days in nests on the surface of damp mud in open tubs, though tadpoles had hatched from the foam on to the mud surface.

The amount of water released by foam collapse was measured by weighing nests, then incubating them till the tadpoles had all emerged, and the foam had collapsed, then reweighing the foam. The results are

Nest number and treatment	Initial weight of foam and eggs (g)	Weight of foam after 56h incubation (g)	Weight of hatchlings (g)	Estimated loss of water from foam (g). In brackets % of original foam weight lost
Closed	1	17.8	2.6	2.1 (13.3%)
	2	14.7	1.3	3.3 (24.6%)
Open	1	13.9	0.7	7.4 (56.1%)
	2	13.6	1.1	8.9 (71.2%)

TABLE 2: Water loss from foam nests incubated in the open, or enclosed. Incubation time is given as hours since laying, estimated as the middle of the night before collection. In calculating water loss, the weight of hatchlings is counted as identical to the initial weight of eggs in the foam.

shown in Table 2. If incubated in the open, water was lost rapidly by evaporation, but if incubated in closed tubs, the nests lost up to a quarter of their original weight by releasing water when the foam structure collapsed.

#### EGG PREDATION

On one occasion on the University of West Indies campus, in a temporary pool filled by heavy rain the previous day, I noticed a large number of *Leptodactylus fuscus* tadpoles apparently feeding on the lower side of a newly-made *P. pustulosus* nest. I took this nest and the tadpoles to the laboratory where this behaviour continued in a glass tank.

To make clear whether both eggs and foam were being attacked, isolated eggs were exposed to potential predators, either floating at the water surface, or sunk to the bottom. The results are shown in Table 3. This very preliminary experiment makes clear that *P. pustulosus* eggs are eaten by *L. fuscus* tadpoles, and by odonate nymphs, but apparently not by large tadpoles of their own species.

Predators	Eggs at start	Eggs left after 24h
3 odonate nymphs	15 floating	4
	15 sunk	6
6 <i>L. fuscus</i> tadpoles	15 floating	0
6 <i>B. marinus</i> tadpoles	15 floating	12
12 <i>P. pustulosus</i> tadpoles	15 floating	15
	10 sunk	10

TABLE 3: Predation of isolated *P. pustulosus* eggs.

#### DISCUSSION

Being in a foam nest could have several effects on an egg's environment: 1. the egg is removed from water and therefore from any water-borne hazards, such as predators; 2. foam may have helpful physico-chemical properties, related to temperature, gas exchange, desiccation or nutrient supply. The following discussion examines which of these effects occur in *Physalaemus pustulosus* nests, and which could have been important in foam nest evolution.

#### TEMPERATURE

Foam could protect eggs from thermal damage (Gorzula, 1977) or keep them warmer than surrounding water, allowing more rapid development (Dobkin and Gettinger, 1985). My data, more complete than the previous authors, support neither suggestion. Foam and water temperatures were very similar, as were times to hatching in foam and floating on water. Rand (1983) notes that Ryan also was unable to detect any thermal effect of the foam, but gives no details of the methods used, and Ryan (1985) himself does not refer to these observations.

From its distribution and habits, *P. pustulosus* was probably a low altitude species originally, breeding in still or slow-moving water, where overheating seems more plausible as a problem than being too cool. Gorzula (1977) measured the temperature of *Physalaemus enesefae* nests at 14.00h, the hottest part of the day, on the two days following oviposition. He found temperature at the centre of the foam mass almost 5°C less than that of adjacent water at a depth of 1cm, and suggested that foam keeps eggs cool to prevent thermal damage. However, Zweifel (1977) showed that anuran embryos, especially those developing in warm climates, rapidly develop tolerance to short term (2-6h) high temperature exposure. For example, by gastrulation, *Scaphiopus couchii* could tolerate 2h at 40°C, and *Bufo cognatus* 6h at 40.5°C. All species were less tolerant during the earliest stages. Although I did not assess temperature tolerance in *P. pustulosus* eggs, it is noteworthy that gastrulation is reached by the first morning, i.e. before any exposure to the sun, and that the maximum temperatures reported for *P. pustulosus* foam are 34°C (Dobkin and Gettinger), 30.8°C (Gorzula) and 35.5°C (this report): all are well below the maximum tolerable temperatures reported by Zweifel.

Dobkin and Gettinger (1985) did not refer to Gorzula's paper, but got the opposite result. They measured the temperature at the centre of three *P. pustulosus* nests, hourly, during the third day of incubation. One nest was in the open, one in shade and one intermediate. When irradiated by the sun, foam warmed more quickly than the surrounding water, becoming 3°C hotter in the unshaded nest at 13.00h. Later, foam cooled more rapidly than water, so that by mid-afternoon, water was warmer than foam in all three nests. Dobkin and Gettinger were surprised at these results, having expected the white foam to reflect solar radiation and keep eggs cool. They worked at an altitude of 600m (my observations were at less than 50m) which may have made a difference. More important, their observations were all during the third day of incubation, when foam structure has altered, and most tadpoles have hatched: the only time I found foam temperature higher than water was on the morning of the third day.

#### DESICCATION

Since *P. pustulosus* nests are deposited at the margins of pools and ditches, attached to vegetation, they are at risk of drying out if the water level falls before the larvae can hatch. Breder (1946) reported seeing *P. pustulosus* (= *Engystomops*) nests stranded on damp mud above the water level, and I have often seen this too. Furthermore, for species like *Bufo marinus* and *Bufo granulosus* which lay egg strings in the same pools and ditches as *P. pustulosus*, water level falls do kill whole clutches of eggs before hatching. Breder and later authors suggested that *P. pustulosus* foam protects eggs from drying out, but no experimental evidence has been published. My results show that the foam does protect eggs from desiccation during the incubation period, but that if the weather is dry, the foam surface dries out, and protection is very limited.

Hatchlings can also survive in the foam, but only if the foam remains wet — as happens if there are showers. Kenny (1969) reports survival of hatchlings in the foam up to 7 days and Rand (1983) quotes 5 days, but neither states the condition of the foam.

Dead embryos at the surface of drying foam have been reported by Moore (1961) in the Australian *Limnodynastes peroni* whose habits resemble *P. pustulosus*. Since surface drying must be common, it would be adaptive for eggs to be mainly deep in the foam mass, rather than evenly distributed, but I have found no evidence for this.

Release of water by collapsing foam late in incubation seems not to have been reported. The water may provide a temporary pool for hatchlings in stranded nests but only briefly if the weather is dry. Breder (1946) noticed a wet streak leading to water from a stranded nest, which he regarded as 'made by the dissolving froth and serving as a path for the escaping tadpoles'. I have not seen this, but sudden release of water by collapsing foam could work this way.

We need to be careful before suggesting anti-desiccation as a primary function of foam — rather than simply necessary once eggs are in foam — since, primitively, eggs were laid in water. Desiccation could have been a problem if the water bodies used by ancestral forms habitually dried out — or if eggs were attached to vegetation and exposed by falling water levels. Although I have seen entire clutches of bufonid eggs perish in dried up pools used also by *P. pustulosus*, these pools may be atypical, since they must be very hazardous for tadpoles too. Indeed, though some tadpole species can survive several days under rocks and leaves if the pool dries up (Downie, 1984), *Physalaemus pustulosus* tadpoles show little of this ability (Downie, unpublished observations). If slow-moving streams were a common original habitat, eggs would be deposited close to the edge, attached to vegetation to prevent currents carrying them away. In the rainy season, streams rise and fall rapidly, presenting a high risk of exposing such eggs, and a means of avoiding desiccation could have been a major advantage.

#### PREDATOR AVOIDANCE

Martin (1967), Heyer (1969) and Ryan (1985) have suggested that foam nests offer protection from predation by removing the eggs from water, but it is clear that protection is not absolute. I found that intact foam nests were attacked by tadpoles of *L. fuscus* and that isolated eggs were predated by aquatic insect larvae and by tadpoles. Moreover, Villa *et al.* (1982) showed that a variety of arthropods, particularly 'frogfly' maggots, specifically predate leptodactylid foam nests — though these are 'new' predators and need not affect the argument that foam nests originally evolved to reduce egg predation. A larger scale study is needed to show whether foam nests have any advantages over other egg protection devices, such as egg toxicity.

There have been reports of tadpoles predated the eggs of other anuran species. After observing *L. fuscus* tadpoles attacking *P. pustulosus* nests, I found that Ryan (1985) had seen a similar attack by *Agalychnis callidryas* tadpoles. Banks and Beebe (1987) have reported that predation of *Bufo calamita* eggs by tadpoles of *Rana temporaria* and *Bufo bufo* is a significant factor in competition between these species. This could also be the case for *L. fuscus* and *P. pustulosus*. *L. fuscus* lays eggs in foam nests in burrows beside temporary pool sites, often in advance of rain (Kenny, 1969; Downie, 1984). When the pool fills, *L. fuscus* tadpoles enter and start to feed, but *P. pustulosus* nests are not deposited till rain has fallen, and are therefore available as food to *L. fuscus*.

#### OTHER FUNCTIONS

The temporary pools used by *P. pustulosus* may become hypoxic on hot still days, given their abundance of micro-organisms and the low solubility of oxygen in warm water. Zweifel (1968) has pointed to the advantages of bufonid egg strings and single eggs at the surface film, over large jelly masses, in such conditions. Presumably, being surrounded by a mass of air bubbles might be even better. This idea needs testing, but since foam nests are deposited on nights following rain, which reaerates ditches and puddles, and the incubation period is only 2 days or so, oxygen lack seems more likely to be a problem for tadpoles than for eggs.

Foam could be a food source for hatchlings, either directly or by offering a substrate for micro-organisms. Kenny (1969) noted that hatchlings may stay up to 7 days in the foam but did not comment on whether they grew. Tanaka and Nishihara (1987) have recently checked this possibility, using *Rhacophorus viridis viridis*, which makes terrestrial foam nests at pond edges. Hatchlings reared in water containing foam grew more than those reared in water with no food source. Tanaka and Nishihara concede that their result is preliminary: they have not tested hatchlings kept in the foam nest itself, not do they know what produces the nutrient effect — the foam itself or micro-organisms involved in foam breakdown. In ground-nesting leptodactylids, Pisano and Del Rio (1968) have suggested that nest foam has growth inhibitory functions, but there is no evidence for this in *Physalaemus*.

#### CONCLUSION

Floating foam nests have been seen (Martin, 1967; Heyer, 1969) as an intermediate stage in the evolution of terrestrial reproduction in the leptodactylids, but they need also to be investigated in their own right. It is surprising, given the abundance, particularly of *P. pustulosus*, how little experimental work has been done on this problem. My results suggest that floating foam does not have important thermal properties, but that anti-desiccation effects do exist. It is also likely that the foam has anti-predator properties, but that this effect is by no means complete.

## ACKNOWLEDGEMENTS

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## SHORT NOTE:

NESTING BEHAVIOUR OF *RHINOCLEMMYS PULCHERRIMA* IN COSTA RICA (TESTUDINES: EMYDIDAE)

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## INTRODUCTION

*Rhinoclemmys pulcherrima* (Gray, 1855) is a semiaquatic emydid turtle which inhabits dry forests from northern Mexico to Costa Rica. Very little is known about its habits, although it is quite abundant in some areas (Pritchard, 1979; Ernst, 1981). This is the first report on its nesting behaviour and is based on three events: a female that nested in 1979, and another that nested in 1980 and 1984. They were kept outdoors in a 100m<sup>2</sup> garden in San José, within the range of the species.

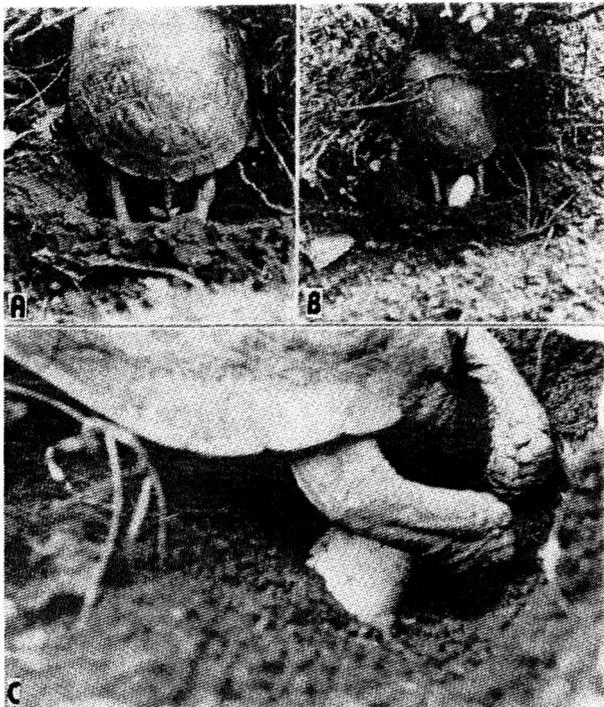


Fig. 1A: Egg-laying begins. Notice the egg partially emerging from the cloaca; B: The relatively large eggs are stacked at the bottom. C: Eggs are covered with dirt.

Females about to nest become more active than usual and apparently search for a place devoid of grass and roots, under bushy vegetation that perhaps serves as camouflage during the nesting process; nesting may occur anytime from May to December (Castillo, 1986), and includes five basic steps. 1. The female anchors herself to the ground by her forelegs and excavates with alternate movements of the hind legs. The claws help fragment the clods, dirt is thrown backwards. She

may stop for short periods, and after about an hour, the hole is about 10cm deep. 2. The tail is oscillated vertically for a few min. 3. A translucent, thick substance begins dropping from the cloaca, and egg laying begins (Fig. 1a). The head is retracted thrice into the carapace each time an egg is laid (N = 1-3 eggs). The interval between deposition of each egg is 2-3 min. In all cases the nests were later found open and the eggs had been destroyed, so we could not measure them, but normally they measure about 4.6 x 2.9cm (Castillo, 1986). 4. These are stacked at the bottom with the legs (Fig. 1b), and tail oscillation continues for about 10 min. after oviposition. 5. She covers the eggs with dirt (small amounts initially) which takes some 25 min. (Fig. 1c). The dirt is initially tamped by the claws of the hind limbs, then by the whole terminal part of the hind limb, with a 'shivering' movement. The body moves in a semicircle, the forelegs serving as axis, which increases the area covered by the hind legs while tamping. Finally, twigs and other debris are added with hind limbs. When the female leaves the nest, the neck is moved as if hiccupping. Steps 1-3 in nesting sequence of *R. funerea* are similar (A. Coto, 1986, pers. com.), and interestingly, *R. punctularia* and *R. diademata* do not dig nests, although their eggs soon become inconspicuous as mud and fallen leaves cover them in the wet forest (Pritchard and Trebbau, 1984). Nest digging is the rule in *R. pulcherrima* (Castillo, 1986) and might have an adaptive function in the dry environments that it inhabits.

## ACKNOWLEDGEMENTS

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## SHORT NOTE:

ULTRACYTOCHEMICAL EVIDENCE FOR THE PRESENCE OF SEROTONIN (5-HT) IN THE PINEAL ORGAN OF *CHALCIDES OCELLATUS* (FORSK.)

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## INTRODUCTION

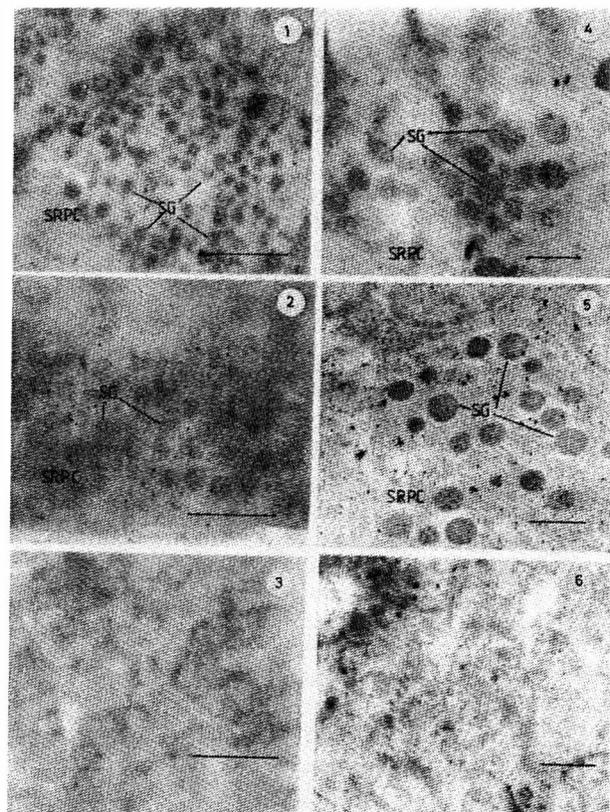
In the pineal organ of lizards the evolutionary regression of photosensory function has been accompanied by tendency to synthesise a number of indoleamines (Colling, 1971, 1979) of these, serotonin has been demonstrated to occur in the pineal organ of *Sauromalus varius* and *Cerrhonotus multicannatus* biochemically by Quay and Wilhoft, 1964; by fluorescence and histochemistry in *Anguis fragilis*, *Lacerta muralis* and *L. vivipara* by Collin, 1968 and by ultracytochemical methods in *L. muralis* by Collin, Juillard and Falcon, 1977.

Numerous secretory granules were demonstrated in the secretory rudimentary photoreceptor cells (SRPC) of the pineal organ of *Chalcides ocellatus* (Mahmoud, 1982). The release of their content by diffusion and/or by micropinocytosis into the capillaries has been demonstrated by Mahmoud, 1982. The aim of the present work was to identify and localise serotonin in the SRPC of the pineal organ of *C. ocellatus*.

The lizards used in this study included members of both sexes, over 9cm mouth-vent length, immediately after decapitation the pineal organ was removed, fixed by immersion and prepared for electron microscopy in accordance with the argentaffin and chromaffin ultracytochemical methods described by Etcheverry and Zieher, 1968; Collin *et al.*, 1977.

With the argentaffin reaction, a precipitate of silver was found over the secretory granules of SRPC (Figs. 1, 2 and 3). As the incubation time increased the silver precipitate became denser, but the background tended to be weaker. Following the chromaffin reaction, whichever fixation procedure was used, similar precipitates of chromium dioxide were found in these granules (Figs. 4, 5 and 6).

The presence of precipitate of metallic silver and chromium dioxide in the secretory granules of the SRPC in the pineal organ of *C. ocellatus* is probably consistent with the occurrence of serotonin in these granules. Similar ultracytochemical observations were reported in *L. muralis* by Collin *et al.*, 1977. Meiniel, Collin and Roux (1975) concluded from *in vitro* and *in vivo* experiments using radioactive  $^3\text{H}$  5-HT that



Figs. 1-6 Argentaffin reaction, precipitate of metallic silver in the SG of the SRPC (Figs. 1 and 2), is absent in control neighbouring cells (Fig. 3). Chromaffin reaction, precipitate of  $\text{CrO}_2$  in the SG of the SRPC (Figs. 4 and 5) is absent in control neighbouring cells (Fig. 6). Incubation time: 2 hrs. Figs. 1 and 4; 4 hrs., Figs. 2 and 3; 5 hrs., 5 and 6. Scale =  $5000\mu$ .

serotonin is stored in the secretory granules of the SRPC in *L. vivipara*.

Further investigations are needed to identify the production and storage site of other indolamines in order to determine the phylogenetic and biosynthetic capacities of the SRPC in *C. ocellatus*.

We would like to thank Prof. J. L. Cloudsley-Thompson, Department of Zoology, University College, University of London, for reading and commenting on the manuscript.

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## SHORT NOTE:

CLUTCH PARAMETERS IN A SWISS POPULATION OF *RANA TEMPORARIA*

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(Accepted 29.10.87)

Egg numbers and egg sizes of anuran amphibians have frequently been shown to vary among individuals and populations, possibly having important demographic and life history consequences. Here I present data on egg numbers and egg sizes from a *Rana temporaria* population 21 km northeast of Berne, Switzerland (elevation 600 m).

During the 1985 breeding season, 16 amplexed pairs of frogs (representing the range of female body sizes) were taken from the breeding pond and each pair set into a plastic container to allow spawning. The volumes of the whole egg masses and of three

subsamples were measured for each pair and the latter preserved in 70% ethanol. The number of eggs in the subsamples were counted, and the total number of eggs per spawn mass was extrapolated from the average ratio of number of eggs to spawn mass volume in the subsamples. In two small egg masses, for which all eggs had been counted, the deviation from the actual number of eggs was less than 4%. From every egg mass the diameters of a sample of 15 preserved eggs were measured with a micrometer eye piece (to nearest 1/100 mm). Yolk volume of an egg mass was calculated as  $n(4/3)(d/2)^3\pi$ ,  $n$  = number of eggs,  $d$  = mean diameter of eggs, assuming spherical shape of the yolk.

Females showed a positive relationship between body length and egg number or egg sizes (Fig. 1). Egg numbers per egg mass ranged from 726 to 1901 and average egg diameters varied from 1.83 to 2.38mm, each with an average range of  $\pm 8.7\%$  ( $\pm 2$  C.V.). The relationship of total volume of yolk produced per egg mass ( $y$ ,  $\text{cm}^3$ ) and body size ( $x$ , mm) was:

$$\log y = -6.01 + 3.59 \log x; n = 16, r = 0.94$$

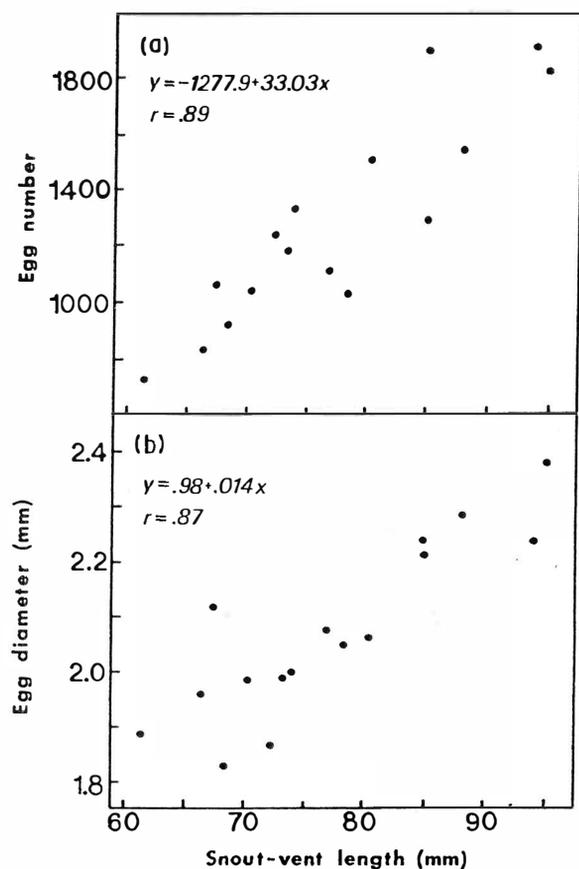


Fig. 1 Relationship between female body length and egg number per clutch (a) and mean egg diameter (b).

The largest female produced  $12.75\text{cm}^3$  of yolk, five times the amount produced by the smallest female ( $2.57\text{cm}^3$ ).

Data on clutch parameters of *Rana temporaria* have been published before by Hönig (1966), Kozłowska (1971), Cooke (1975), Kminiak (1975), Koskela and Pasanen (1975), Jørgensen (1981), Hintermann (1984), Cummins (1986) and Gibbons and McCarthy (1986), but not all authors give the body length-egg number and -egg diameter relationships, making quantitative comparisons difficult.

Body length accounts for about 75-80% of individual variation in egg numbers and egg sizes. A high correlation is typical for egg numbers, but correlation is usually lower for egg diameters. Residual variation in clutch parameters may be explained by environmental differences, experienced by individual frogs (Kaplan, 1987). Additionally, age differences

may account for some of the variation in egg sizes (Gibbons and McCarthy, 1986). Comparison with other populations reveals considerable differences in both egg numbers and egg sizes that cannot be explained by body size differences. Frogs in an Irish population show a similar range of egg numbers and larger egg diameters (about 2.1-2.6mm), despite about 10mm smaller body sizes (Gibbons and McCarthy, 1986). English frogs can have close to 4,000 eggs despite smaller body sizes (Cummins, 1986), and Danish frogs produce eggs of only about 1.1-1.9mm despite similar body length (Jørgensen, 1981). These deviations may partially be due to environmentally induced year-specific variation (Cummins, 1986, Kaplan, 1987), or in the case of egg sizes, to methodological differences. But the considerable variation suggests that populations differ in their trade-off between egg numbers and egg sizes (Smith and Fretwell, 1974) or in total investment. Variation in clutch parameters therefore probably reflects different local selection pressures or environmental constraints, such as water temperatures, length of growing season, predation or competition.

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## SHORT NOTE:

RECORDS OF TWO SPECIES OF *HYLARANA* (ANURA: RANIDAE)

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## ABSTRACT

The genus *Hylarana* Tschudi is recorded and described for the first time for Zambia on the basis of specimens of *Hylarana darlingi* and *Hylarana galamensis* respectively. Specimens of the former species came from Livingstone and Monze districts whereas the latter species was collected from Chilubi island, Lake Bangweulu. *Hylarana galamensis* (Dumeril and Bibron) attains a larger body size (SVL) than that of *H. darlingi* (Boulenger).

## INTRODUCTION

The genus *Hylarana* Tschudi is made up of what are commonly referred to as Golden backed or white-lipped frogs. The genus is widespread and is distributed throughout Africa south of the Sahara to Indonesia (Poynton and Broadley, 1985). Various species are known to inhabit a variety of habitats from forests to grassland and including swamps. Our present knowledge of the genus and the African species within the genus is based mainly on the work by Perret (1977) who reviewed the species of *Hylarana* known to occur in Cameroon and provided a list of the African species.

There are presently three species in the genus *Hylarana* known to occur in Zambia i.e. *H. lemairi*, (recently reported by Poynton and Broadley, 1985), *H. darlingi* and *H. galamensis*. Previous to the period of collection, i.e. 1975 and 1976 respectively, species in genus *Hylarana* were not known to occur within Zambia and indeed at the time when the Zambian checklist was published (Broadley, 1971) there was no definite record of the genus from Zambia. Two species are being described for the first time on the basis of one adult female specimen of *H. galamensis* and eight specimens (3 adult females and 5 males) of *H. darlingi*. Attempts to secure more specimen of the former species were in vain.

## MATERIALS AND METHODS

The only available specimen of *Hylarana galamensis* was collected at Chilubi island, Lake Bangweulu (11° 11'S and 30° 01'E) by Mike Bingham in 1975. Later in the year, Mr. Bingham donated this lone adult female specimen to the Livingstone Museum. Efforts to acquire more specimens failed because of lack of funds.

Collecting expeditions were mounted around Livingstone district (17° 37'S and 25° 51'E) and Monze district (16° 7'S and 27° 29'E) respectively. This collecting venture was successful and resulted into

collection of yet another new species within the genus *Hylarana* never before recorded in Zambia. General description of these two species, based on preserved specimens housed in the Livingstone Museum, Zambia are given.

*Hylarana galamensis* (Dumeril and Bibron 1841).

*Hylarana galamensis* (Dumeril and Bibron)  
*Rana galamensis*: Dumeril and Bibron 1841:367. Lake Galam, Senegal. Holotype in the Museum Natural d'Histoire Naturelle, Paris. Boulenger 1907: 481, Parker, 1930:897.

*Limnodytes bravanus*: Peters 1882:9 Brava, Somalia. Type lost.



Fig. 1 *Hylarana galamensis*, adult female, general view.

*Rana galamensis bravana*: (Peters), Poynton, 1964a: 121 and 1964b: 204, Stewart, 1967:62.

An adult female specimen catalogue number NMZL 164 housed in the National Museum, Livingstone was collected at Chilubi island in Lake Bangweulu, northern province, Zambia.

#### DIAGNOSIS

A broad dorsal golden to brown band present. This brown band is demarcated by almost immaculate to heavily speckled area but usually leaving higher margin which overlies a pair of flattered ridges running from eyes to leg insertions. Flanks are light-spotted to marbled. Abdomen speckled, but less markedly so in adult specimens. Males have a pair of baggy, darkly pigmented gular pouches, that open through a pair of slits parallel to the mandible. Tips of fingers are not expanded into discs and generally the distance from nostril to eye is equal to interorbital distance (see Poynton and Broadley, 1985). Males are known to reach 78mm, females 86mm. The adult female specimen described herein had snout-vent length of 65.7mm.

#### HABITAT

Strongly aquatic species, that is restricted to permanent swamps and lakes.

#### DISTRIBUTION

Known to occur on Chulubi island. But it has also been recently recorded at Mpulungu and Nyamkolo (Poynton and Broadley, 1985). This represents an extension to the species range.

*Hylarana darlingi* (Boulenger, 1902).

*Rana darlingi* Boulenger, 1902:15. Monze and between Umtali (Mutare) and Marandellas (Marondera), Zimbabwe. Syntypes in the British Museum (N.H.), London, Broadley, 1971:113, Stevens, 1974:7.

*Hylarana darlingi* (Boulenger), Poynton, 1964a:119, Perret 1977:843.

Female specimen of *H. darlingi* in the National Museum of Zambia at Livingstone, catalogue number NWZL 303. Collected at Sinde River, Livingstone by Dr. M. P. Simbotwe and Mr. A. S. Muyundu on 30th March, 1976. Two adult female specimens of *H. darlingi* catalogue number NMZL 790 and NMZL 786 and five adult male specimens catalogue numbers, NMZL 783, 784, 785, 787, 789 were collected at Luyaba, Malundu and Keemba dams in Monze district, Zambia.

#### DIAGNOSIS

A broad golden to light brown band extends from the snout and backwards over head and upper eyelids to above vent (Poynton and Broadley, 1985). The glandular skin ridge not as conspicuous as in *H. galamensis*. Flanks fairly uniformly dark brown to olive. A white line runs from above the axilla below the tympanum and eye to the narial region. Adults are usually virtually immaculate below apart from light



Fig. 2 *Hylarana darlingi*, adult female, general view.

spotting on legs. Males have pouches that are barely developed and tips of fingers not expanded into discs. Males not normally exceeding 55mm, females not exceeding 63mm (Poynton and Broadley, 1985). Three female specimens, had snout-vent length ranging from 45 to 49mm whereas snout-vent length for five males ranged from 45 to 51mm.

#### HABITAT

This species inhabits open savannas and is strongly associated with permanent streams and dams. It has also been recorded in lowland evergreen forest at the Lusitu lagoon (Poynton and Broadley, 1985).

#### DISTRIBUTION

*H. darlingi* occurs in great abundance in Livingstone and Monze districts of Southern Zambia, but it has also recently been recorded from Kalabo, Lutakila R., Mpika and 16km W of Chisamba.

## DISCUSSION

I recommended that the search for new and previously unrecorded species of amphibians in Zambia should be endorsed under the forthcoming countrywide natural resources inventory project under implementation by the National Conservation Secretariat (NCS). *H. galamensis* should be sought for in Northern Zambia where it is expected to be widespread whereas *Hylaran darlingi* and *H. lemairei* may prove to be widespread in western, southern, central and northern provinces of Zambia. Further distribution records are necessary for all these species in order to ascertain their habitat range and extent of geographic distribution within Zambia.

## ACKNOWLEDGEMENTS

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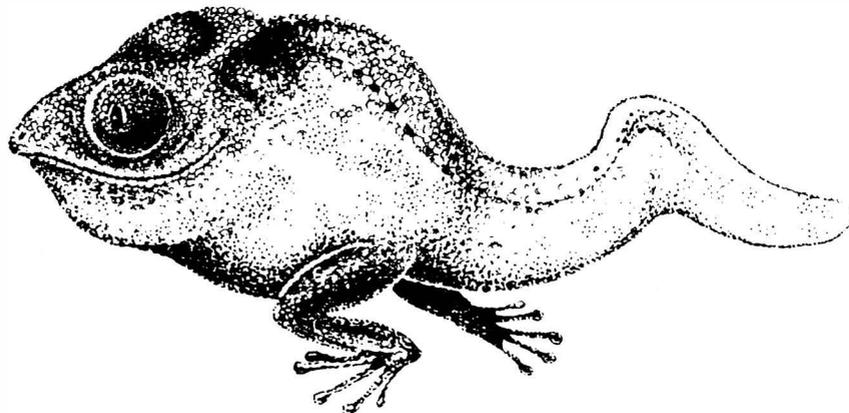
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