THE HERPETOLOGICAL JOURNAL

FORMERLY THE *BRITISH JOURNAL OF HERPETOLOGY*

ANNOUNCEMENTS

The World Congress of Herpetology announces the

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This international congress will be the first of a series occurring at regular intervals at venues around the world. Such a meeting will enable all persons interested in herpetology to meet and exchange information to promote the advance of knowledge and the conservation of the world's amphibians and reptiles. The congress will consist of topical symposia, poster sessions, plenary speakers, workshops, displays, excursions, and meetings of ancillary groups. Subjects and moderators of symposia will be announced well in advance so that potential participants can volunteer. The meeting will be open to all persons. Registration will begin 1 January 1988.

For further details and mail listing, write: Dr. Ian R. Swingland, World Congress of Herpetology, Rutherford College, University of Kent, Canterbury, Kent CT2 7NX, United Kingdom.

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FRONT COVER: Sexual selection: Natterjacks *Bufo calamita* in amplexus.

REVIEW:

SEXUAL SELECTION AND BODY SIZE IN AMPHIBIANS

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ABSTRACT

Sexual behaviour in amphibians is very diverse and variable. We examine Shine's (1979) conclusion that large male body-size is associated with combat and suggest that such a simplistic analysis is inadequate. We review briefly the recent literature and conclude that a full understanding of the role of sexual selection in amphibians requires a greater knowledge of variability in mating behaviour, alternative mating strategies, life history patterns, particularly growth, and physiological constraints on sexual behaviour.

INTRODUCTION

Sexual selection is that component of natural selection that favours characters giving individuals an advantage in competition with members of the same sex in terms of greater reproductive success. Evidence for the action and consequences of sexual selection is of two kinds, behavioural data on the dynamics of competitive and sexual behaviour in living animals, and comparison of the morphology of living species, with particular emphasis on sexual dimorphism.

Many amphibians are very suitable subjects for collecting data on the dynamics of mating behaviour since many of them form large, localised mating aggregations. In terms of morphology, several species provide an example of sexual dimorphism that is particularly challenging to sexual selection theory. It is widely assumed that, where males fight for access to females and larger males are at an advantage in fights, males will tend to be larger than females. In many anurans, fighting occurs in which there is a strong large-male advantage, but males are considerably smaller than females.

This topic has previously been reviewed by Shine (1979). In this paper we provide an alternative approach to Shine's, which we find flawed in several respects, as well as a review that takes into account more recent data and developments in sexual selection theory.

CRITIQUE OF SHINE (1979)

In his review, Shine (1979) concluded that, in most amphibian species, females are larger than males but that, in those species in which males compete for females, male size may approach or exceed that of females. In support of this conclusion, Shine listed published data on the incidence of male combat and on body size for many anuran and urodele species. He clearly recognised some of the limitations of this approach, stating that while use of these data on sexual

size differences introduces some error it has the compensating advantage of enabling me to include data from a large number of species' (p. 300).

To assess the value of Shine's data, we have consulted the papers that he cites. We suggest that the data on body-size are too inconsistent to permit statistical analysis of the kind that he used. Some authors give body-size data as snout-vent length, others as total length. In some papers, data are given as mean with variance, either with (e.g. Brame, 1968) or without the sample size (e.g. Mecham, 1968). Where given, sample sizes vary greatly. Some authors give mean body-lengths only (e.g. Peacock and Nussbaum, 1973), others give only the ranges for each sex (e.g. Highton, 1962). Data derived from fresh specimens are compared with material in museum collections, taking no account of shrinkage due to preservation (Lee, 1983; Verrell, 1985a). In some cases, authors discuss the possibility that there is geographical variation in body size (e.g. Rubenstein, 1969). For one genus, *Oedipina*, Student's t-tests on the original data (where sample sizes permit) show there to be no significant size differences between the sexes, although Shine states that, in three of the seven species listed, the female is larger than the male (data from Brame, 1968).

In his analysis, Shine ostensibly compared species in which males fight with those in which fighting is absent. However, inspection of his Table 1 reveals that he compared species with fighting with those in which it may or may not occur ('not recorded in these species', p. 300). Nearly all the primary sources cited are concerned with ecology, few of the authors being specifically concerned with sexual behaviour. It is clearly important in an analysis like Shine's that species be categorised as being definitely with or without fighting.

Shine acknowledges that the species he considers have very diverse natural histories, but he does not allow for confounding variables that might arise from inter-taxon comparisons. For instance, he compares species that breed on land with aquatic-breeding

species and he takes no account of marked variations between species in the duration of the breeding season. He also compares territorial with non-territorial species. Among urodeles, true territoriality has, to date, been described only in the terrestrial plethodontid salamanders. Studies in both the field (e.g. Jaeger, 1971) and the laboratory (e.g. Thurow, 1976) suggest that, in these urodeles, there is both inter- and intra-specific aggression in which both sexes participate. Large body-size is advantageous to individuals, of either sex, in aggressive encounters. In one species, *Plethodon glutinosus*, the male defends a territory against other males but allows females to enter for mating (Wells, 1980). Shine states that combat does not occur in this species and that the female is larger than the male. In fact, fighting between males is likely, and authors differ as to whether the female (Highton, 1962; Peacock and Nussbaum, 1973) or the male (Rubenstein, 1969) is the larger sex, or whether they are of equal size (Pope and Pope, 1951).

There are several other uncomfortable exceptions to Shine's conclusions which cannot be dismissed as statistical 'noise'. In the European toad, *Bufo bufo*, the breeding season is short (about 14 days) and scramble competition between males for females is intense (Davies and Halliday, 1979). Fights are frequent, vigorous and prolonged and, as clearly shown by both laboratory experiments and field data, there is a clear advantage to larger males, because they can both displace smaller males from the backs of female and can defend females more effectively against rivals (Davies and Halliday, 1977, 1979). Despite this clear advantage to large male size, males are substantially smaller than females (Davies and Halliday, 1979). As discussed below, this example shows that sexual dimorphism in body size is the result of a variety of selective forces and cannot be attributed solely to sexual selection.

We also question Shine's emphasis on 'combat' as a behavioural manifestation of inter-male competition. In many urodeles, males severely reduce the mating success of rivals by various forms of sexual interference (e.g. Arnold, 1976; Verrell, 1984). There is no evidence that body size has an influence on the effectiveness, either of sexual interference, or of a male's ability to counter it (sexual defence). In anurans, there have been several recent studies of mating dynamics that have considered body-size as an important determinant of male mating success but which have found other factors to be more important (see below).

Explanations for the evolution of body-size must take into account the effects of life-history and age, because amphibians typically continue to grow throughout life. This could create a misleading impression of sexual dimorphism if, within a population, members of one sex are larger than the other simply because they are older. This possible explanation for sexual dimorphism in body-size was considered by Organ (1961) in his study of *Desmognathus*, but is not considered in Shine's analysis.

Finally, we are critical of the emphasis that Shine places on body-size and on weapons used by males

during fighting. There are many other morphological features in which the sexes are dimorphic, notably in the many and varied glands of male urodeles and, more specifically, the bright colours and elaborate crests of European nexts (*Triturus*) and the premaxillary teeth of certain plethodontids (Arnold, 1977). In anurans, males of many species have a highly-developed vocal apparatus and produce complex and energetically-expensive vocalisations.

The comparative method is a widely-used and potentially powerful means for testing hypotheses about the adaptive significance of specific characters, but is one that must be used with caution (Clutton-Brock and Harvey, 1984). We suggest that Shine's analysis violates at least two of the limitations of the method identified by Clutton-Brock and Harvey: that numerical estimates extracted from the literature be accurate, and that there be an awareness that body size is correlated with a large number of behavioural and ecological variables.

URODELES

Among urodeles, sexual dimorphism in body-size is generally slight or absent and it is usually the female that is the larger sex. In 35 genera listed by Shine (1979), the female is larger in 16, the male in 8 and males and females are of equal size in 11. Vigorous and prolonged fighting appears to be rare in urodeles, though good data are scarce, and there seem to be no species that have evolved specialised structures for fighting. It is noteworthy that in three species in which fighting between males has been described recently, *Notophthalmus viridescens* (Verrell, 1986a), *Paramesotriton hongkongensis* (Sparreboom, 1984) and *Salamandra salamandra* (Kastle, pers. comm.), males are smaller than females, contrary to Shine's conclusion.

There are many other aspects of sexual dimorphism than body size, and many more ways of competing than by overt fighting. Sexual interactions in urodeles involve the transfer of secretions from male to female and males in many species develop very large glands in the breeding season, usually on the head, and perform elaborate movements by which the male applies his glands to the female's snout (Arnold, 1977; Arnold and Houck, 1982). In *Triturus*, male odour is water-borne and is transferred to the female by fanning, a rapid movement of the tail (Halliday, 1974). The male's courtship pheromone is produced by the dorsal gland (also referred to as the abdominal gland), one of a number of glands opening into the male's cloaca (Malacarne *et al*, 1984). In the breeding season, the dorsal gland increases in size dramatically, in some males representing 10 per cent of their total body weight (Verrell *et al*, 1986). *Triturus* courtship also involves visual displays and the genus is highly unusual among urodeles in that males develop elaborate decorations in the breeding season, including a large dorsal crest and conspicuous skin patterns (Halliday, 1975, 1977).

The most fully-described form of sexual competition between males is sexual interference, whereby males disrupt the courtship behaviour of rivals. This takes a

variety of forms, including moving between a courting male and a female and displaying to her, mimicking female behaviour so as to induce a male to deposit a spermatophore that will not be picked up, and depositing a spermatophore on top of that of a rival. Sexual interference has been described in two ambystomatids, *Ambystoma maculatum* and *A.tigrinum* (Arnold, 1977), a plethodontid, *Plethodon jordani* (Arnold, 1977), and two salamandrids, *Triturus vulgaris* (Verrell, 1984) and *Notophthalmus viridescens* (Verrell, 1982a, 1983). It may have evolved independently in each of these families, or may have arisen in a common ancestor, in which case it is an extremely ancient pattern of behaviour. Sexual interference is a form of mating competition in which large body-size does not confer any advantage. Small males can interfere as effectively as large males and the effectiveness of behaviour patterns by courting males that counteract its effects (sexual defense) is not dependent on body-size. Territoriality in plethodontids may be a form of sexual defence since it will exclude potential rivals from the mating area. In *Plethodon vehiculum* aggression is more strongly associated with mating activity than with the defence of food resources (Ovaska, in press). In this genus, however, males are smaller than or equal in size to females (Shine, 1979).

The significance of sexual interference and other forms of male competition as a source of variance in male reproductive success is uncertain, because its frequency depends largely on the dynamics of natural breeding populations, about which little is known. In this context, what is important is not the overall sex ratio, but the operational sex ratio, defined by Emlen and Oring (1977) as the ratio of sexually active males to sexually responsive males. Our recent study of *Triturus vulgaris* in the field suggests that the operational sex ratio can change markedly during the breeding season, from an excess of females at the beginning to an excess of males later on when females start egg-laying and become unreceptive (Verrell and Halliday, 1985). Field observations by one of us (PAV) suggest that, as we predict, sexual interference is more frequent in the later part of the season when active males greatly outnumber receptive females. The only other study of changes in the operational sex ratio during the season is that of *Ambystoma jeffersonianum* by Douglas (1979), who found that sexually active males always outnumbered receptive females, but more so early in the season.

Body size is an important determinant of reproductive success in urodeles, in both sexes, because it is correlated with measures of fecundity, oocyte number in females, testis size in males (Verrell *et al*, 1986). While body size is generally correlated with age, the relationship explains only a small proportion of the total variance in body size (Halliday and Verrell, in press). Much more important is the variation that exists within age-classes, suggesting that the major determinant of body size is growth before the age of first reproduction.

Another factor that will affect male reproductive success is the rate at which spermatophores can be produced. In *Triturus vulgaris*, males show a decline in their daily spermatophore production over the course of a season (Halliday, 1976) and males require more than 24 hours to replenish their supply of available spermatophores (Verrell, in press). Spermatophore production rate will be an important determinant of male reproductive success for several seasons. First, if it is slow, males may frequently encounter females at times when they have little or no sperm with which to inseminate them. Secondly, male display rate is correlated with spermatophore supply (Halliday, 1976) and, because males must display at a high rate if they are to attract females (Teyssedre and Halliday, 1986), their chances of inseminating females will be reduced while they are replenishing their spermatophore supply. Finally, because females store sperm and may mate with more than one male, sexual selection may take the form of sperm competition, though there is as yet little direct evidence that this is a significant factor in urodeles (Halliday and Verrell, 1984).

Evidence for mate choice in urodeles has been sought but has proved elusive, and there is clearer evidence for choice by males than by females. Males of both *Triturus vulgaris* (Verrell, 1986) and *Notophthalmus viridescens* (Verrell, 1982b, 1985b) show a preference for larger, more fecund females. Female choice is manifested in *T. vulgaris* by a greater tendency to pick up spermatophores deposited by males that produce several than from those that put down a few (Halliday, 1974, 1983), and by their being more responsive to males that display at a high rate (Teyssedre and Halliday, 1986).

In conclusion, variance in the reproductive success of male urodeles is a product of several factors, including the operational sex ratio, the ability to produce spermatophores, mate choice and the development of epigamic characters. If body size is important, its significance lies not in fighting but in its relationship to fecundity. The complexity of the determinants of mating success in urodeles is illustrated by a recent, detailed study of *Desmognathus ochrophaeus* (Houck *et al*, 1985). This showed that there is variance in the mating success of both sexes, more markedly among males, but did not reveal any morphological correlate of such variation.

ANURANS

Mating systems among frogs and toads are both diverse and, within species, highly variable, making it difficult to classify them into mutually exclusive categories (Wells, 1977a; Arak, 1983a). Interspecific differences are related largely to variation in the duration of the breeding season; species with a very short season (explosive breeders) tend to show scramble competition resulting in random mating, those with the longest seasons tend to have a territorial system in which males defend mating and/or spawning sites. Between these extremes there is a variety of patterns, perhaps the most common being a lek-like system in which males defend calling sites but not resources. Within species, variation can be considerable, both between populations and, within a

population, between years. Such variation is a function of variation, not only in breeding season duration, but also population density and operational sex ratio (Arak, 1983a).

Within-species variation in mating dynamics may have important consequences for the intensity with which sexual selection acts on males. For example, a switch in male behaviour, from calling to females from fixed positions to active searching and fighting for females, has been described for *Bufo canorus* (Kagarise-Sherman, 1980) and *B. calamita* (Arak, 1983a) and, in both cases, is associated with a high population density. Such a switch may mean that different male characters are favoured by sexual selection at different times and in different places: call characteristics when density is low, mobility and strength when it is high. Theoretical discussions of sexual selection typically envisage a powerful, sustained and one-directional selection pressure as being a necessary condition for the evolution of an elaborate or extreme male character. The behavioural plasticity observed in many anurans will tend to mitigate against such conditions.

Another factor tending to reduce the intensity and uni-directionality of sexual selection in anurans is the existence, in many species, of alternative male mating strategies. Arak (1983a) identifies two types of alternative strategy, depending on the type of mating system. In species in which males fight for females, the alternative strategy is to search for unpaired females. In those in which males attract females by calling or by defending resources, it is to adopt silent or non-territorial 'satellite' behaviour. In many cases, the alternative strategy is shown by males that are inherently less competitive, most commonly because of small body-size. In calling species, however, satellite behaviour may be adopted temporarily by males that have become exhausted after a period of sustained calling (Ryan, 1985; Robertson, 1986a). The relative frequency of individuals adopting an alternative strategy is largely dependent on total population density and may thus be very variable, in both time and space (Arak, 1983).

The intensity of sexual selection on males pursuing a primary mating strategy with partly depend on the relative mating success of individuals adopting an alternative strategy; the more successful the alternative strategy, the less strongly will the primary strategy be favoured. In *Hyla cinerea*, calling males and non-calling satellites experience approximately equal mating success (Perrill *et al*, 1978); in *Bufo calamita* satellites are less successful than callers (Arak, 1983a).

In species in which males fight to obtain and defend females, it has commonly been found that larger males have higher mating success. Examples include: *Bufo americanus* (Gatz, 1981), *B. bufo* (Davies and Halliday, 1979), *B. woodhousei* (Woodward, 1982) and *Rana sylvatica* (Howard, 1980). In all these species, as in the majority of anurans, males are smaller than females (Woolbright, 1983). It seems clear, therefore, that whatever the strength of sexual selection favouring large body-size in males, it is not as strong as selection for large size in females. This conclusion was reached for *Rana sylvatica* by Howard and Kluge (1985). We

agree with Woolbright (1983) that the adaptive value of large size in females arises from its positive correlation with fecundity, but disagree with him that males are smaller than females because of energetic constraints (see also Sullivan, 1984). Skeletochronological data for *Bufo bufo* suggest that males reach sexual maturity at least one year before females (Gittins *et al*, 1982; Hemelaar, 1983). Annual growth rate appears to be much faster in anurans before the onset of breeding than it is during adult life (Halliday and Verrell, in press), and this may well account for the larger body size of females in breeding populations.

It has been suggested that body size (usually measured as snout-vent or snout-urostyle length) is not the most significant correlate of male mating success. Howard and Kluge (1985) present evidence that male arm-length is more important in *Rana sylvatica* and suggest that males with longer arms can maintain a more secure grip on females.

While several studies of anuran mating patterns have sought evidence for a large-male advantage, many have found that the most significant correlate of male mating success is the amount of time for which males are present at a breeding site. This effect has been shown for *Bufo calamita* (Arak, 1983b), *B. woodhousei* (Woodward, 1982), *B. rangeri* (Cherry, pers. comm.), *Hyla chrysoscelis* (Godwin and Roble, 1983), *H. rosenbergi* (Kluge, 1981), *H. cinerea* (Gerhardt, pers. comm.), *Centrolenella fleischmanni* (Greer and Wells, 1980; Jacobson, 1985) and *C. prosoblopon* (Jacobson, 1985). In *Rana clamitans*, higher mating success falls to those males that spend the most time in good-quality territories, in terms of their suitability for oviposition (Wells, 1977b). A correlation between mating success and time spent in mating activity may be due to the latter being a function of variance in the ability of males to meet the physiological demands of mating activity. That sexual and competitive behaviour is energetically expensive for male anurans is suggested by data indicating substantial weight losses during the mating period (Arak, 1983a; Robertson, 1986a; Wells, 1978), and by studies of the energetics of mating behaviour (Bucher *et al*, 1982; MacNally, 1981; Ryan *et al*, 1983; Sullivan and Walsberg, 1985; Taigen and Wells, 1985; Wells and Taigen, 1984).

An alternative way by which larger males could gain a mating advantage is if they are preferred as mates by females (Halliday, 1983b). Female choice for larger males has been reported for *Bufo americanus* (Fairchild, 1984), *B. quercicus* (Wilbur *et al*, 1978), *B. woodhousei fowleri* (Fairchild, 1981), *Hyla crucifer* (Gatz, 1981b; Forester and Czarnowsky, 1985), *H. marmorata* (Lee and Crump, 1981), *H. versicolor* (Gatz, 1981b), *Physalaemus pustulosus* (Ryan, 1980), *Rana catesbeiana* (Emlen, 1976; Howard, 1978) and *R. clamitans* (Ramer *et al*, 1983). In many of these cases, it is suggested that the adaptive advantage of female choice for larger males is that they will tend to mate with males that are older and, therefore, of proven survival capacity. We suggest that, because age and size are generally only weakly correlated in anurans, the adaptive value of larger males is more likely to lie in their rapid early growth (Halliday and Verrell, in press).

Several studies have obtained evidence for females choice on the basis of individual variation in the male advertisement call. In some species, the fundamental frequency of the call is inversely correlated with body-size, providing a cue by which females could potentially mate preferentially with males of a specific size. Such a preference, for larger males, has been reported in *Physalaemus pustulosus* by Ryan (1985) and Robertson (1986b) has found that female *Uperoleia rugosa* use call frequency to identify and mate preferentially with males whose weight is approximately 75 per cent of their own. Several other studies have found a tendency by females to approach calls with features that indicate high energy expenditure by the males that produce them. Females prefer high intensity (louder) calls in *Bufo calamita* (Arak, 1983a) and *Hyla versicolor* (Fellers, 1979), calls with a high repetition rate in *Bufo woodhousei* (Sullivan, 1983), calls of long duration in *Hyla regilla* (Whitney and Krebs, 1975), and calls that contain extra components in *Physalaemus pustulosus* (Ryan, 1985). Whether or not such preferences are adaptive for females is uncertain (Halliday, 1983b). Males that produce more energetically expensive calls may be fitter than other males, in terms of their ability to survive, and such fitness may be heritable, but this has yet to be demonstrated. At present, a more parsimonious explanation is that females are attracted to those calls that provide the most powerful stimulus or which are easiest to locate.

CONCLUSIONS

Amphibian mating systems are not as simple as they might appear to the casual observer; this is arguably the only generalisation it is safe to make about them. Attempts, such as that by Shine, to find correlations between behavioural and morphological characters are not useful, because they fail to take into account the diversity and variability of amphibian behaviour, or the variety of factors that have influenced their evolution. In particular, it is becoming increasingly apparent that body-size in amphibians cannot be explained solely in terms of sexual selection; because body-size is related to fecundity and age, its evolutionary basis must be sought through an understanding of life history. Recent studies have also shown that it can be misleading to categorise the sexual behaviour of any given species. Amphibian behaviour is very variable and is highly influenced by the dynamics of a breeding population which, in turn, vary in both time and space. The situation is further complicated by the existence in many species of alternative male mating strategies, the effect of which is to diminish the extent to which any one category of male achieves higher mating success. These are often rather subtle forms of behaviour that are revealed only by intensive observation.

We suggest that studies of amphibian sexual behaviour, if they are fully to reveal the effects of sexual selection, must address three aspects. First, many amphibians are long-lived and breed more than once. Natural selection acts on lifetime reproductive success which may or may not be accurately estimated from observations made in a single season. There is a need for more studies that measure male reproductive success over several seasons. Secondly, body-size is an important determinant of reproductive success in many species, but the factors that are important in its evolution are poorly understood. Sexual selection may play some part, but more needs to be known about the factors that regulate growth in amphibia. Finally, there is increasing evidence that amphibian sexual behaviour is subject to physiological constraints and that these may be what limits male mating success. Such constraints include respiratory limits on display in urodeles and calling in frogs and the rate at which spermatophores are produced in urodeles. To understand the role of sexual selection in amphibians, behavioural biologists will need to turn to the considerable knowledge being gathered by physiologists.

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NOTES ON THE MORPHOMETRICS AND SPOT PATTERNS OF FEMALE SMOOTH NEWTS (*TRITURUS VULGARIS*) AT A COASTAL SITE IN LINCOLNSHIRE

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ABSTRACT

Adult female *Triturus vulgaris* breeding at seven small ponds within a freshwater marsh at Saltfleetby-Theddlethorpe Dunes National Nature Reserve were measured, weighed and examined for throat and belly spotting.

When the data were combined it was found that 26.8 per ent $\pm$ 4.2 per cent S.E. of the total population had immaculate throats. Immaculate-throated newts tended to have fewer, smaller and usually less distinct belly spots than the normal spotted-throated form. All the immaculate-throated newts in the sample were found to have dark-yellowish throat and lower mandible pignmentation.

There were no significant morphometric differences between immaculate-throated and spotted-throated newts at the study site although the immaculate-throated animals were found to have a significantly shorter head + body length than those recorded in mid-Wales by Harrison, Gittins and Slater (1981). Both immaculate-throated and spotted-throated newts at the study site were found to be significantly lighter than those recorded by Frazer (1983) and Harrison *et al.* (1981).

It is suggested that the high incidence of immaculate-throated female smooth newts at Saltfleetby-Theddlethorpe Dunes NNR is the result of the 'founder effect'.

INTRODUCTION

It is well known that the females of the two smaller British newt species, *Triturus helveticus* and *Triturus vulgaris*, are not easily distinguished from one another in the field. Frazer (1983) states that the females of both species have 'much the same range of brown and olive colouration with a whitish belly'. Although it is generally stated that they can be separated by the paler immaculate throat of the palmate female (Smith, 1964; Arnold, Burton and Ovenden, 1978; Frazer, 1983), Smith (1964) states that the spots or speckles on the throats of some smooth newts may be very indistinct and easily overlooked. A number of workers have reported female smooth newts which have been difficult to interpret (De Fonseca and Jocqué, 1982; Frazer, 1983) and low incidences of immaculate-throated females of this species have been recorded in some populations (Roberts, pers. comm.). However, as far as the writer is aware there is little reported work quantifying their frequency in natural populations. This short paper describes the occurrence of immaculate-throated female smooth newts at the Saltfleetby-Theddlethorpe Dunes National Nature Reserve in Lincolnshire and compares the morphometrics of these animals with those of the normal form.

THE SITE

The Saltfleetby-Theddlethorpe Dunes National Nature Reserve is situated on the north Lincolnshire coast 20 miles south of Grimsby (Grid Ref. TF472915). A feature of the site is the extensive freshwater marsh, extending to approximately 12 hectares, which is dominated by a combination of fen/marsh and relict saltmarsh plant species. This marsh contains a number of small artificial ponds, most of which have been created over the past 10 years as part of a programme to improve the breeding habitat of the natterjack toad (*Bufo calamita*). The freshwater marsh has usually dried up by midsummer and these ponds provide areas of permanent fresh water which support large populations of common frog (*Rana temporaria*), common toad (*Bufo bufo*) and smooth newt (*Triturus vulgaris*) during the breeding season. The palmate newt (*Triturus helveticus*) has not so far been recorded at the site. The pH of the ponds ranges from 6.5 to 8.0 and each has an established emergent vegetation of spike-rush (*Eleocharis uniglumis*), blunt-flowered rush (*Juncus subnodulosus*) and reedmace (*Typha latifolia*).

It is not certain how long *Triturus vulgaris* has been present on the nature reserve but the reserve records show that the species was first recorded between 1965 and 1969 and a preliminary survey of the amphibia of the site in August 1973 (Hutton, 1973) found larvae of this species to be numerous in most of the ponds of the freshwater marsh. Casual observations since then have indicated that a relatively high proportion of the adult female newts in the population are immaculate-throated animals.

METHODS

To obtain quantitative information on the frequency of this morphological variant within the population, samples of adult female newts were taken from each of seven discrete ponds within the freshwater marsh at the peak of breeding activity between 26th and 30th March 1984. Care was taken to ensure that ponds geographically close to one another, and between which there may have been some movement of animals, were sampled on the same day and usually within the same hour, to minimise the possibility of any individual animal being captured more than once. Sampling was carried out during daylight using a long-handled, coarse-mesh pond net for sweeping emergent vegetation and catching newts in open water. Only female newts actually in the water were sampled as it was assumed that these would be adult animals. Each captured newt was weighed and measured; the length of tail, from the posterior edge of the cloaca to the tip, and the head + body length were measured to the nearest millimetre using a transparent plastic rule. The standard error (S.E.) was calculated for each measurement and 95 per cent confidence limits were attached using Student's 't' to allow for the small sample. After drying off excess moisture, the weight of each animal was recorded to the nearest 0.1 g. using a 'Pesola' spring balance and the throat and lower mandible were carefully examined to determine whether markings were present or not. Additionally, belly markings were noted and categorised as follows:

Category 1 without markings

Category 2 small spots or speckles $\leqslant$ c. 1.0mm diam.

Category 3 Blotches $>$ c. 1.0mm diam.

In general newts fell easily into one of the three belly marking categories. Only three newts intermediate between categories 2 and 3 were captured and in each case it was possible to allot each animal to a category once belly markings had been counted and measured.

Statistics derived from the biomial distribution were used to estimate the proportion of the population with immaculate throats, with the standard error (S.E.) being calculated as $\sqrt{(pq/n)}$, where p is the proportion of animals with immaculate throats, $q = 1 - p$ and n is the sample size. The relationship between belly markings and the presence or absence of throat spots was examined using a Chi-square (x^2) test for association.

RESULTS

In total, 112 randomly selected adult female *Triturus vulgaris* were captured from the seven ponds and examined for the presence or absence of throat spotting. Due to the small samples from each pond the data were combined and statistical analysis showed that 26.8 per cent ± 4.2 per cent S.E. of the total population of adult female newts had immaculate throats.

The belly markings of a sample of 100 newts were recorded and categorised as detailed above. The results of this investigation are given in Table 1. As only three

Belly markings	Numbers of newts	
	Throats spots	Immaculate throats
Immaculate	2	3
Small spots/speckles $\leqslant$ c.1.0mm diam.	43	21
Blotches $>$ c.1.0mm diam.	29	2

TABLE 1: Belly and throat markings of adult female *Triturus vulgaris* at Saltfleetby-Theddlethorpe NNR, Lincolnshire.

completely immaculate newts (with both immaculate belly and throat) and only two immaculate-bellied animals with throat spots were captured it was not possible to use the Chi-square test to examine the relationship between the presence or absence of throat spotting and belly spotting. However, when the Chi-square statistic was used to examine the relationship between the relative size of belly spots and the presence or absence of throat spotting it was found that newts with immaculate throats tended to have category 2 belly markings, i.e. small spots ($x^2 = 7.91$; p <0.05). Although no actual counts of belly spots were made, other than for newts which were intermediate between classes 2 and 3, 81 per cent of the sample of immaculate-throated newts were classified as having 'small spots or speckles'.

Table 2 shows the average lengths and weights of both immaculate-throated and normal spotted-throated newts. There was not a significant difference in overall length, head + body length, tail length or weight. The ratio of tail length to head + body length was 0.89 for immaculate-throated newts and 0.85 for those with spotted throats.

DISCUSSION

Although immaculate-throated female smooth newts appear to be quite well known to workers on the genus *Triturus* in Britain (Halliday, pers. comm.) their frequency in natural populations has not been well documented. The little data available suggest that only small numbers of adult female smooth newts within any one population are likely to have immaculate throats (Roberts, pers. comm.). The frequency within the Saltfleetby-Theddlethorpe population is therefore surprisingly high.

Frazer (1983) states that there is no significant difference in size between adult females of *Triturus vulgaris* and *Triturus helveticus* and this is supported by the work of Bell (1966) in Leicestershire. Casual observations at Saltfleetby-Theddlethorpe NNR between 1979 and 1983, later supported by the quantitative data collected in 1984, suggested that there was not a noticeable difference in overall size between spotted-throated and immaculate-throated female newts and it was at first thought that the latter might be *Triturus helveticus*. Closer examination of these animals during the 1984 field work showed that they had two layers of pigmentation on the throats, a dark yellowish background pigmentation, usually with

Throat markings	Total length (mm)			Head + body length (mm)			Tail length (mm)			Weight (g)		
	mean	n	95% limits	mean	n	95% limits	mean	n	95% limits	mean	n	95% limits
Spotted throat	78.5	82	1.3	42.3	82	0.7	36.2	82	0.8	1.7	74	0.1
Immaculate throat	77.9	30	2.4	41.3	30	1.1	36.6	30	1.5	1.7	25	0.2

TABLE 2: Comparative size data for adult female *Triturus vulgaris* with spotted and immaculate throats at Saltfleetby-Theddlethorpe NNR, Lincolnshire.

Ratio Location	Total length (mm)			Head + body length (mm)			Weight (g)			Ratio tail length: body length
	mean	n	95% limits	mean	n	95% limits	mean	n	95% limits	
Llysdinam — 1981 (Harrison *et al.* 1981)	80.1	175	0.8	43.4	175	0.5	2.3	41	0.16*	0.85
Llysdinam — 1981-83 (Harrison *et al.* 1984)	79.8	266	0.63	—	—	—	—	—	—	0.83
Leicestershire (Bell, 1966)	75.9	—	—	—	—	—	3.4	81	—	—
Ham Street (Frazer, 1983)	—	—	—	—	—	—	2.25	20	0.23*	—
Other sites in mid-Wales (Harrison *et al.* 1984)	82.2	13	3.27*	—	—	—	—	—	—	—

TABLE 3: Size data for adult female *Triturus vulgaris* at a number of other sites in Britain.
95% confidence limits have been calculated for the data of Harrison *et al.* (1981 and 1984) and Frazer (1983).
The figures marked with an asterisk have been calculated using Student's 't' to allow for the small samples.

a layer of spots or speckles on top of this. In agreement with the work of Roberts (pers. comm.) all the immaculate-throated newts in the sample from Saltfleetby-Theddlethorpe NNR were found to have this yellowish background pigmentation. As *Triturus helveticus* has a pale pink throat due to lack of pigmentation, it was concluded that the Saltfleetby-Theddlethorpe animals were not this species.

The possibility that these immaculate-throated female newts might be hybrids between *Triturus vulgaris* and *Triturus helveticus* was also considered. However, although partially viable hybrids between the two species have been produced in the laboratory (Spurway, 1953), only one natural hybrid has been recorded in the wild as far as is known (Griffiths, Roberts and Sim, In prep.) and other investigations of presumed hybrids have been shown to be morphological variants of *Triturus vulgaris* (Freytag, 1970; Roberts, pers. comm.). The fact that not a single specimen of *Triturus helveticus* was found during the intensive sampling at Saltfleetby-Theddlethorpe and the knowledge that there is not, as far as is known, a colony of this species in reasonable proximity to the Reserve supports the conclusion that the immaculate-throated animals at this site are also a morphological variant of *Triturus vulgaris*.

Data are available from Bell (1966), Frazer (1983) and Harrison, Gittins and Slater (1981, 1984) on the morphometrics of adult female smooth newts and these are summarised in Table 3. Harrison *et al.* (1981) give mean lengths and weights together with standard deviations, as do Harrison *et al.* (1984) for overall lengths only and Frazer (1983) for weights only. For the purposes of direct comparison 95 per cent confidence limits have been calculated for these data. A comparison of Tables 2 and 3 shows that there is no significant difference in the average overall lengths of either spotted-throated or immaculate-throated newts at Saltfleetby-Theddlethorpe and those measured by Harrison *et al.* (1981) and Harrison *et al.* (1984). Similarly, spotted throated newts at Saltfleetby-Theddlethorpe NNR were not found to be significantly different from the smooth newts measured by Harrison *et al.* (1981) with regard to weight and head + body length. However, immaculate-throated newts at Saltfleetby-Theddlethorpe were found to have significantly shorter head + body length, at the 95 per cent level of confidence, than those recorded by Harrison *et al.* (1981) and both immaculate-throated and spotted-throated newts at Saltfleetby-Theddlethorpe were found to be significantly lighter at the same level of confidence, than those recorded by Frazer (1983) and Harrison *et al.* (1981). Bell (1966) gives only mean overall length and mean weight data for female smooth

newts from his Leicestershire site but it seems likely that both immaculate-throated and spotted-throated newts at Saltfleetby-Theddlethorpe are significantly lighter than those measured in Leicestershire. Weight comparisons should however be treated with extreme caution due to the problems of female newts carrying differing numbers of eggs at the time of weighing. In agreement with the work of Bell (1966) all the newts measured at Saltfleetby-Theddlethorpe NNR were found to have head + body length greater than tail length.

Roberts (unpublished data) suggests that spot size, number and colour can be highly variable both within and between populations. At Saltfleetby-Theddlethorpe immaculate-throated female smooth newts were found to have fewer, smaller and usually less distinct belly spots than those with normal spotted throats, suggesting that they are generally less melanic than the normal form, in agreement with the trends found in Roberts's data.

When a site is relatively isolated it is usually the case that the colonisation of an empty habitat involves only small numbers of individuals. Under such circumstances the colonising event will give rise to a marked change in allele frequencies and in alleles present in the descendent population. This is unlikely to be significantly affected by fresh variation introduced by later immigration (Berry, 1977). The comparative isolation of the freshwater marsh at Saltfleetby-Theddlethorpe NNR from other suitable smooth newt habitat suggests that the high incidence of immaculate-throated adult female smooth newts may perhaps be the result of this 'founder effect', with the initial colonisers carrying genes which favoured immaculate throats.

ACKNOWLEDGEMENTS

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THE DISTRIBUTION OF NEWTS, *TRITURUS* SPP., IN THE PEAK DISTRICT, ENGLAND

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ABSTRACT

1. Surveys of the distribution of newts, *Triturus* spp. in the Peak District show a distinct geographical separation between the species. *T. vulgaris* and *T. cristatus* occur principally on the Carboniferous Limestone, in ponds of pH >7.0. *T. helveticus* occurs on the Carboniferous Millstone Grit and Shales in more acid ponds of pH <7.0.

2. However, the altitudinal distribution of these species shows that *T. helveticus* is not a 'montane' species, as has been alleged, but occurs mostly in ponds below 1000 ft (305m), whereas *T. vulgaris* and *T. cristatus* occur mostly in ponds above that height.

3. Both field work and inspection of the 1:25,000 O.S. maps indicate an abundance of small field ponds suitable as breeding ponds for *T. vulgaris* and *T. cristatus*. Though population sizes in any one pond may be small, the overall density of ponds suggests that total population are high, and of no immediate conservation concern.

INTRODUCTION

The Palmate Newt, *Triturus helveticus*, is more numerous and widespread in northern and western Britain, leading Smith (1954) to suggest that it was a more montane species than the Common Newt *Triturus vulgaris*. Others have subsequently observed, however, that *T. helveticus* is not especially characteristics of high altitudes (Cooke and Ferguson, 1975) but that it is much more tolerant of acidity and lower ionic concentrations (Cooke and Frazer, 1976).

The Peak District provides an ideal area to examine further these opposing ideas. In the south, the dome of Carboniferous Limestone (the 'White Peak') produces a high plateau of base-rich rock dissected by lower dales. In the north and around the western and eastern flanks of the limestone area, the very acid rocks of the Millstone Grit (the 'Dark Peak') also produce high plateaux, interrupted by valleys of equally acidic Shales and Coal Measures. Thus both low and high altitude situations are available on both acidic and basic rocks.

In view of the concern which has been expressed for the survival of amphibian populations in southern Britain (e.g. Beebee, 1973; Cooke, 1972; Presst, Cooke and Corbett, 1974), a survey of the area for newts provided also an opportunity to consider the status and prospects for amphibians in this area.

METHODS

Information comes from three sources. In 1974-76, a preliminary survey was undertaken to establish the whereabouts of ponds with amphibian populations. Effort was principally directed at newts, and small ponds, which could be reasonably sampled with a pond net in 15 minutes netting, were preferred. In 1976, efforts were made to examine all the ponds shown on the First Series 1:25,000 Ordnance Survey maps in a few limited sampling area. This preliminary survey thus provides information on relative numbers of newts of the three species (*T. helveticus, T. vulgaris* and the Crested Newt *T. cristatus*) and also on the survival or otherwise of ponds marked on those maps (which date from surveying carried out in the period 1889-1935, but mostly from 1900-1920).

In 1984-85, and consequential upon the results obtained by Cooke and Frazer (1976), a sample of the ponds surveyed in 1974-76 was revisited. Newts were again sampled by 15-minute pond netting, and the pH of each pond ascertained with a portable Kent EIL 3055 digital pH meter. Three readings were obtained from each pond, and the mean of these three used in analysis. The approximate altitude of each pond (to the nearest 50 ft contour, from the 1″ (1:63,600) Ordnance Survey map, the geology, physical characteristics (size, shape, depth) and other features (fauna and flora of the pond, nature of surrounding habitat) were also noted.

The third source of information is the Ordnance Survey maps of the area, especially the First Series 1:25,000 maps and, for the White Peak, the Second Series 1:25,000 tourist map. These give some information on the number of potential breeding sites available, and also, perhaps, on the level of change seen between the First Series (surveyed 1889-1935 but mostly 1900-1920) and the Second Series (surveyed 1950-1976). The availability of ponds was scored from the First Series maps for the whole of the 10 km squares SK05, 06, 07, 08, 09, 15, 16, 17, 18, 19, 25, 26, 27, 28, 29; SJ96, 97, 98; and SE00. Thus this availability relates to an area somewhat larger than,
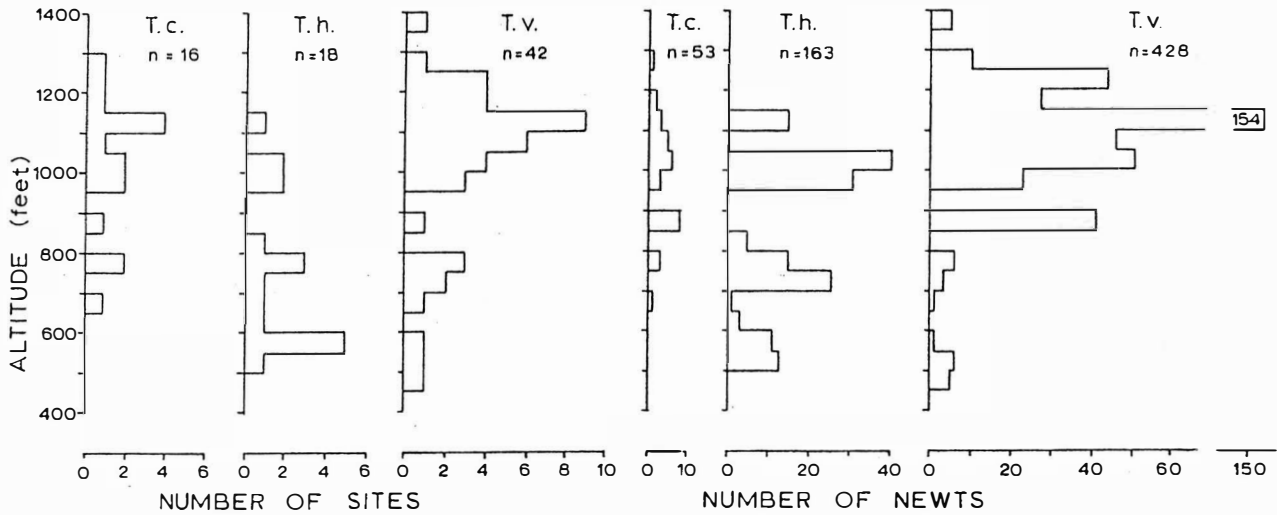
Fig. 1 Altitudinal distribution of newts *Triturus* spp. in the Peak District
(a) by the ponds in which they were found
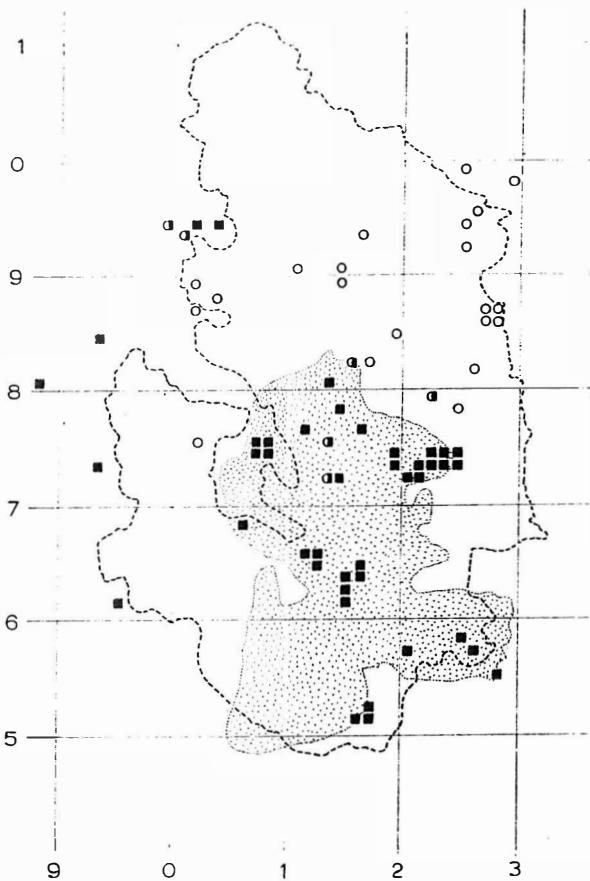(b) by numbers of individual newts handled.

Fig. 2 Distribution of newts *Triturus* spp. in the Peak District. The grid squares represent the 10 km National Grid, and the dashed line is the outline of the Peak District National Park. The stipple indicates the extent of the Carboniferous Limestone o *T. helveticus* ■ *T. vulgaris*. (*T. cristatus* not mapped, for security).

though encompassing almost all of, the Peak District National Park. For examining changes between the First and Second Series maps, a more limited sample of 10 km squares, SK 15, 16, 17, 25 and 26, was used; these contained the majority of the ponds in the Peak District. Ponds were scored as 'Field Ponds' — mostly in fact 'dew ponds' created for stock, but also other small ponds, and 'Reservoirs' — larger bodies of water, mostly reservoirs but also large ornamental lakes and similar ponds which could not be adequately sampled for newts but which were, in any case less likely to be used by them (because of the presence of large fish and other predators).

RESULTS

STATUS OF THE AMPHIBIANS

T. vulgaris is much the most common newt, with 439 handled at 42 sites in all. *T. helveticus* is numerous (148 handled at 15 sites), while *T. cristatus* is apparently much scarcer, though fairly widespread (52 handled at 16 sites) (Table 1). The relative abundance in the two surveys was similar; although the proportion of sites which had newts was higher in the second survey, this was simply because this was a resurvey of sites found in the first survey, and therefore concentrated on better sites.

All the sites at which *T. cristatus* was found also contained *T. vulgaris*; none of them contained *T. helveticus* as well, though one pond containing all three species is known near Calver (D. Whiteley, pers. comm.). Three sites contained both *T. helveticus* and *T. vulgaris*.

Of the other two amphibians, the Common Frog *Rana temporaria* is also abundant in this area and occurs nearly twice as commonly as *T. vulgaris*. Since most records are of spawn or tadpoles, it is not possible to present numbers of individual frogs for comparison with the newts. The Common Toad *Bufo bufo* appears to be relatively scarce, being recorded from only eight

sites. However, it generally favours larger water bodies than the small ponds which were the primary target of this survey, and is likely to be more numerous locally than this suggests. In his report of amphibians in the Sheffield area, which includes much of the Peak District, Whiteley (1977) had 655 sites for *Rana* and 338 for *Bufo*.

ALTITUDE

The 18 sites where *T. helveticus* occurred ranged from 500-1,100ft in altitude, but only three sites were above 1,000ft (305m), and the median height was only 700ft (213m) (Table 2); thus, most sites were in the shale valleys, at fairly low altitudes. The 42 sites with *T. vulgaris* occurred in a similar range, 450-1,250ft, but because most of them were up on the limestone plateau, the median height was 1,050ft (320m); the difference was statistically highly significant (Mann-Whitney U-test, p<0.0001). Since all the *T. cristatus* sites were also *T. vulgaris* sites, it is not surprising that these two species occupied a similar altitudinal range (Fig. 1).

GEOLOGY AND pH

The distribution of the two species differed markedly; 15 out of 18 ponds with *T. helveticus* were on gritstone, whereas only nine of the ponds with

T. vulgaris were on the gritstone (Table 2). The three ponds which had both species included two of those where *T. helveticus* occurred on limestone. Since *T. cristatus* invariably shared its pond with *T. vulgaris*, it is not surprising to find that it, too, occurred principally on the limestone (Fig. 2). The different preferences, of *T. helveticus* for the gritstone and *T. vulgaris* for the limestone, were statistically highly significant (X^2 test, p<0.00006).

Since pH is largely a reflection of this geological difference, it is not surprising that, in the smaller sample of ponds checked for pH, there was also a clear bias of *T. helveticus* toward more acid ponds and *T. vulgaris* (and *T. cristatus*) toward more basic ponds. Both of the smaller species occurred over a wide range of pH, and with a considerable overlap, but only three of the ponds with *T. helveticus* had a pH of 7.0 or more; two of these were ponds with *T. vulgaris* also present. Conversely, only three of the ponds with *T. vulgaris* had a pH below 7.0; the other 'shared' pond was one of these. Again, *T. cristatus* occurred in ponds of high pH, with a suggestion, not statistically significant, that it might prefer ponds which were on average more base-rich than those frequented by *T. vulgaris*. The difference in observed pH between *T. helveticus* and *T. vulgaris* was highly significant (Mann-Whitney U-test, p<0.002).

	1974-76 Survey		1984-85 Survey		Total	
	No. of Ponds	No. of Newts	No. of Ponds	No. of Newts	No. of Ponds	No. of Newts
T. helveticus	11	89	12	59	15	148
T. vulgaris	34	210	24	229	42	439
T. cristatus	11	33	7	19	16	49
Ponds surveyed	142	—	45	—	163	—
Ponds with newts	36	—	33	—	51	—
Ponds with no newts	106	—	12	—	112	—
Ponds with *Rana*	59	—	23	—	70	—
Ponds with *Bufo*	7	—	3	—	8	—

TABLE 1: Abundance of Newts, *Triturus* spp., during two surveys of the Peak District. Number of newts determined by 15 min. pond net sampling at each site. Because many sites found in 1974-76 were revisited in 1984-85, the total number of ponds known to hold each species is less than the total of the two columns.

	Altitude (ft)		pH		Geology (No. of ponds)	
	Median	Range	Median	Range	Limestone	Grit/Shale
T. helveticus	700	500-1100	6.7	4.7-8.1	3	15
T. vulgaris	1050	450-1250	7.6	5.7-9.7	33	9
T. cristatus	1000	650-1150	7.9	7.3-9.7	14	2

TABLE 2: Altitude, pH and underlying geology for breeding ponds of newts *Triturus* spp. in the Peak District.

T.h. v T.v.	U = 138; z = 3.899; p = 0.0001	U = 53; z = 3.063; p = 0.002	$x^2_1 = 20.12$; p = 6 x 10^5
T.h. v T.c.	U = 46; z = 3.420; p = 0.0006	U = 8; z = 3.095; p = 0.002	$x^2_1 = 17$; p = 6 x 10^4
T.v. v T.c.	U = 324; z = 0.219; p = 0.826	U = 66; z = 1.333; p = 0.182	$x^2_1 = 0.6$; p = 0.56

It should, perhaps, be added that measurement of pH in the field was an unpredictable or erratic procedure. The comparison in the preceding paragraph was based on the mean, for each pond, of three or four readings. In 23 ponds, out of the 37 newt-ponds measured, the three readings were all within 0.5 pH units, giving some confidence in the value of the mean for this comparison (given that the species' preferences were 0.9 pH units apart). The other 14 ponds produced readings more variable than this, however, with in the extreme case 2.08 pH units discrepancy. These larger discrepancies presumably reflect local photosynthetic or respiratory activity, with bicarbonate forming or dissociating, perhaps only in the neighbourhood of the probe, but they could equally indicate genuine differences in the environment experienced by the newts. In other words, though the difference in average pH favoured by the species is real, all species must be tolerant of a range of ionic concentrations.

AVAILABILITY OF PONDS

Study of the 1:25,000 maps reveals several paradoxes. Because the Carboniferous Limestone is so porous, and liable to dry out in summer, large numbers of field ponds (dew ponds) have been dug. Some of these still have the traditional lining of clay with limestone blocks embedded in it for protection, but many are now lined with concrete. Conversely, the Gritstone region, because it is impervious, rarely dries out completely, even in the most severe drought, so livestock always has access to water; there has, therefore, been little or no need to dig artificial ponds. There is, therefore, the paradox that, in the dry Limestone area, newts have a wealth of suitable breeding ponds available, whereas in the wet Gritstone such ponds are apparently in short supply (Table 3). It was certainly difficult to find enough ponds on the Gritstone to sample for *T. helveticus*, and the sample size of ponds with that species is small, whereas the ponds sampled for *T. vulgaris* are only a small selection of those that could have been examined. It is probable that the surveyors were more punctilious about

recording the clearly artificial dew ponds, on the limestone, than they were about recording the sites (ditches, natural oxbow lakes, etc.) that newts tend to use in the Gritstone areas; in other words, the real availability of breeding sites for *T. helveticus* is probably greater than the figures in Table 3 imply.

A second paradox is that the Gritstone has conversely, a much higher number of large ornamental lakes and water-supply reservoirs; obviously these would not be constructed over the porous limestone. Though these large water bodies are likely to be unsuitable for newts (and certainly impossible to sample properly for newts), they tend to have associated with them settling pools, water channels and similar smaller water bodies which may well be suitable for newts (but may not be shown separately on the maps).

The even higher density of newt ponds on the Cheshire Plain is the result of excavating marl ponds. However, this area was not examined for newts, and is not considered further.

The survival of ponds through to recent times is indicated in two ways — from the survey in 1976 of a sample of ponds marked on the First Series maps, and from comparing the First Series with the Second Series. Of 101 ponds visited in 1976, 20 had dried up or been filled in and were therefore 'lost' as newt ponds; however, only 85 of this 101 were shown on the First Series maps, the remaining 16 were 'new' ponds and almost balanced the losses. Comparing the two series of maps also suggests a modest loss (Table 3b), with 71 per cent of the ponds shown on the older maps still extant according to the newer maps. Here too there are suggestions that the situation is actually better than the new maps indicate. Firstly, the revising surveyors seem to have been more restrictive in what they mapped; of 50 ponds shown on the First Series maps, and still evident in 1976, 13 were omitted from the Second Series. If this level of under-representation applies throughout the newer maps, the 'corrected' number of ponds actually available for newts now may be no less than when the First Series maps were drafted.

(3a)	Area Covered	No. of Field Ponds	Density of Field Ponds	No. of Lakes & Reservoirs	Density of Lakes & Reservoirs
Limestone	560 km²	1006	1.80/km²	44	0.08/km²
Gritstone	1245 km²	449	0.36/km²	208	0.17/km²
Cheshire Plain	95 km²	649	6.83/km²	20	0.21/km²

(3b)	No. of Field Ponds	No. of Reservoirs	No. of Field Ponds	No. of Reservoirs
	First Series		Second Series	
Limestone	893	36	628	11
Gritstone	19	13	16	15

TABLE 3: The availability of ponds in the Peak District:
(a) as shown on the First Series 1:25,000 maps, for twenty 10 km squares;
(b) as shown, for a sub-sample of five 10 km squares, on the First and Second Series 1:25,000 maps.

Secondly, there were 10 ponds in this sample that were not shown on either series of maps, (and another two ponds, not shown on the First Series, that had correctly been added to the Second Series maps). In other words, there are more ponds available for newts than the maps suggest.

DISCUSSION

The ditribution of the three *Triturus* species in the Peak District shows very clearly that while *T. vulgaris* and *T. cristatus* inhabit the base-rich Carboniferous Limestone area, with ponds of high pH, *T. helveticus* is not a montane species in any sense of that adjective; on average, it occurs at lower altitude than the other two species. Though he did not analyse the altitudinal records to emphasise the point, Whiteley (1977) pointed out these same distinctions in distribution.

Cooke and Ferguson (1975) examined the national distribution records for an altitudinal difference in range between *T. helveticus* and *T. vulgaris*, and could find, at most, only a hint that *T. helveticus* might be more numerous at higher altitudes. For this, they used the 400ft contour as the dividing line between lowland and highland, but they only had five records of newts above 1,000ft. They concluded that altitudinal preferences were, at most, only a marginal factor in explaining the tendency to a northwestern/southeastern division between *T. helveticus* and *T. vulgaris*, and felt that underlying substrate was more important. This suggestion was strongly supported by the more detailed study of pH preference undertaken by Cooke and Frazer (1976), and by this study.

In the absence of earlier surveys of the Peak District, it is difficult to be certain that there have been no major declines in amphibian populations. However, this survey suggests that the two smaller newts are still common and widespread. The Crested Newt *T. cristatus* is of concern to conservationists, in particular because of declines in S.E. England (e.g. Beebee 1973, 1975, 1977). Though the numbers handled in this study were small, the ponds were small and unlikely to hold large populations; the largest was 29 x 37m, but most were dew ponds 7m in diameter. There were, however, enough of these ponds, scattered widely throughout the limestone region, to suggest that the total population is large and not endangered. Though the 1976 survey of sites shown on the 1:25,000 map found that there had been some losses of ponds, perhaps 25 per cent of those marked on the maps, it also found a similar number of 'new' ponds. Given that the predominant land use on the limestone is for grazing cattle or sheep, and that much of the soil is too shallow for ploughing, the ponds are likely to remain in existence (though there is a trend towards piped water supplies and drinking troughs). Although much of the limestone plateau is intensively farmed and neat, the dale sides are generally covered in rougher vegetation, providing ample terrestrial habitat for newts. In the gritstone areas, rough grazings and heather (grouse) moorland are the main land uses, so that there is, again, no shortage of suitable habitat.

ACKNOWLEDGEMENTS

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THE INTRINSIC INNERVATION OF THE MALE REPRODUCTIVE SYSTEM OF A FRESHWATER TURTLE *TRIONYX GANGETICUS* (CUVIER). A BREEDING CYCLE STUDY

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SUMMARY

The intrinsic nerve supply of the male reproductive system of *Trionyx gangeticus* has been studied by histological and histochemical methods. Thin nerve fibres penetrate the tunica propria and enter the cellular portion of the seminiferous tubule. Some nerve fibres are also associated with blood vessels and interstitial cells. Nerve endings are observed in close association with interstitial cells. The functional relationship of the nerve supply to interstitial cells is discussed. The nerve supply of the testis differs along with the changes that occur in the testis. During the breeding season, no clear-cut asssociation of nerve fibres, either with vessels or with Leydig cells, could be established. Acetylcholinesterase-positive nerve fibres are present in the testes surrounding each seminiferous tubule. Cholinesterase activity is mainly restricted to the intertubular space. The epididymis and vas deferens contain few nerve fibres and the density of innervation differs in different regions of the spermatic duct is discussed.

INTRODUCTION

Autonomic influence may be far more widely involved in the regulations of reproductive process and in their dysfunction than has been generally recognised. There can be little doubt of the prime importance of the central nervous system in sexual activity, even though the details regarding which are still far from clear. Many workers who studied the innervation of the testes and their respective ducts in mammals had divergent views with respect to the distribution of nerve fibres (Kuntz, 1919; Mitchell, 1938; Okkels and Sand, 1940; Shioda and Nishida, 1966). Tingari and Lake (1972) extended the list of species investigated to birds. Unsicker (1973) observed adrenergic nerve fibres in the testicular interstitial tissue in reptiles. However, the knowledge regarding the innervation of the entire reproductive system of reptiles is incomplete. The present investigation is intended to add to the existing knowledge on this aspect with a study on the distribution of nerve fibres in the testis and spermatic duct of the male freshwater turtle *Trionyx gangeticus* during its reproductive cycles.

MATERIAL AND METHODS

Ten adult male turtles were purchased in every month during 1979-1981 from a local market, which were captured from the Betwa river (22° 32' N, 77° 51' E) located at 45 km north of Bhopal, India. They were immediately killed by chloroform anesthesia after being brought from the market. The reproductive organs were removed and small pieces of the tissues were fixed in Bouin's fluid and of the three reproductive organs in 10 per cent formalin for both histological and neurohistological studies. Routine paraffin sections were obtained and stained with haematoxylin and eosin for histology. Bielschowsky (1902) staining method modified by Davenport *et al* (1934) was followed to study the neurohistology.

To study the cholinesterase activity, 30-35 μm fresh frozen sections of the testis and spermatic duct of two breeding turtles were taken and were stained according to the method of Koelle and Friedenwald (1949), modified by Coupland and Holmes (1957). In order to stain selectively for specific (Ache) and non-specific (Che) cholinesterase, butyrylthiocholine was substituted for acetylthiocholine as a substrate and eserine was used as inhibitor.

RESULTS

The testis of turtle *Trionyx gangeticus* seems to be richly innervated as is evident by the presence of many thick and thin fibres. In the stretch preparation the covering of the testis, the tunica albuginea, is provided with a good number of nerve fibres extending for a considerable distance (Fig. 1). The blood vessels of the testis are also traversed by a few fine nerve fibres. The majority of the nerve fibres, as they encircle the testis, are accompanied by arteries. Many fine branches of testicular nerves are located in the interstitial tissue. Some of the nerve fibres are associated with blood vessels. Nerve endings are observed in close association with interstitial cells (Fig. 2). However, penetration of nerve fibres to the individual Leydig cells could not be traced.

Acetylcholinesterase-positive nerve fibres around the seminiferous tubule can be seen (Fig. 3). The cholinesterase-positive activity is seen in the intertubular spaces (Fig. 4). There is no evidence, however, of any nerve penetration into the tubules. Some of these nerve fibres terminate near the Leydig cells.
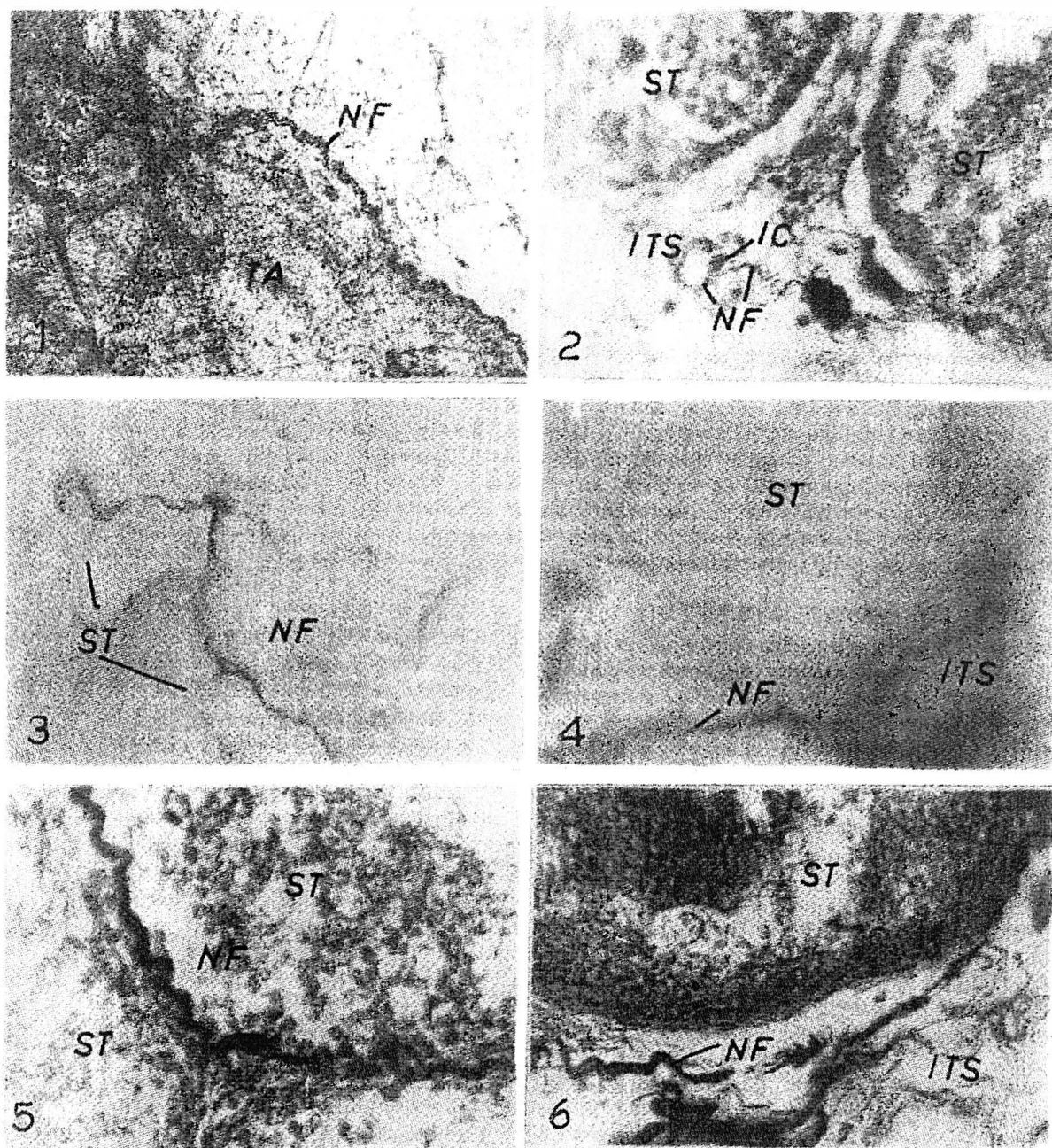
PLATE 1

Fig. 1 Stretched preparation of the tunica albugenia (TA) showing nerve fibres (NF) passing on the surface of tunica albuginea.

Fig. 2 Nerve fibres (NF) in the intertubular space (ITS). Note the nerve endings in association with the intertitial cells (IC). Seminiferous tubule (ST).

Fig. 3 Acetylcholinesterase positive nerve fibres (NF) passing around the seminiferous tubules (ST).

Fig. 4 Acetylcholinesterase positive activity in the interstitial tissue (ITS). Note the nerve fibre (NF) in between the seminiferous tubules (ST).

Fig. 5 Nerve fibres (NF) passing around the enlarged seminiferous tubule (ST).

Fig. 6 Nerve fibres (NF) around the seminiferous tubule (ST). Note the nerve fibres in the intertubular space (ITS).
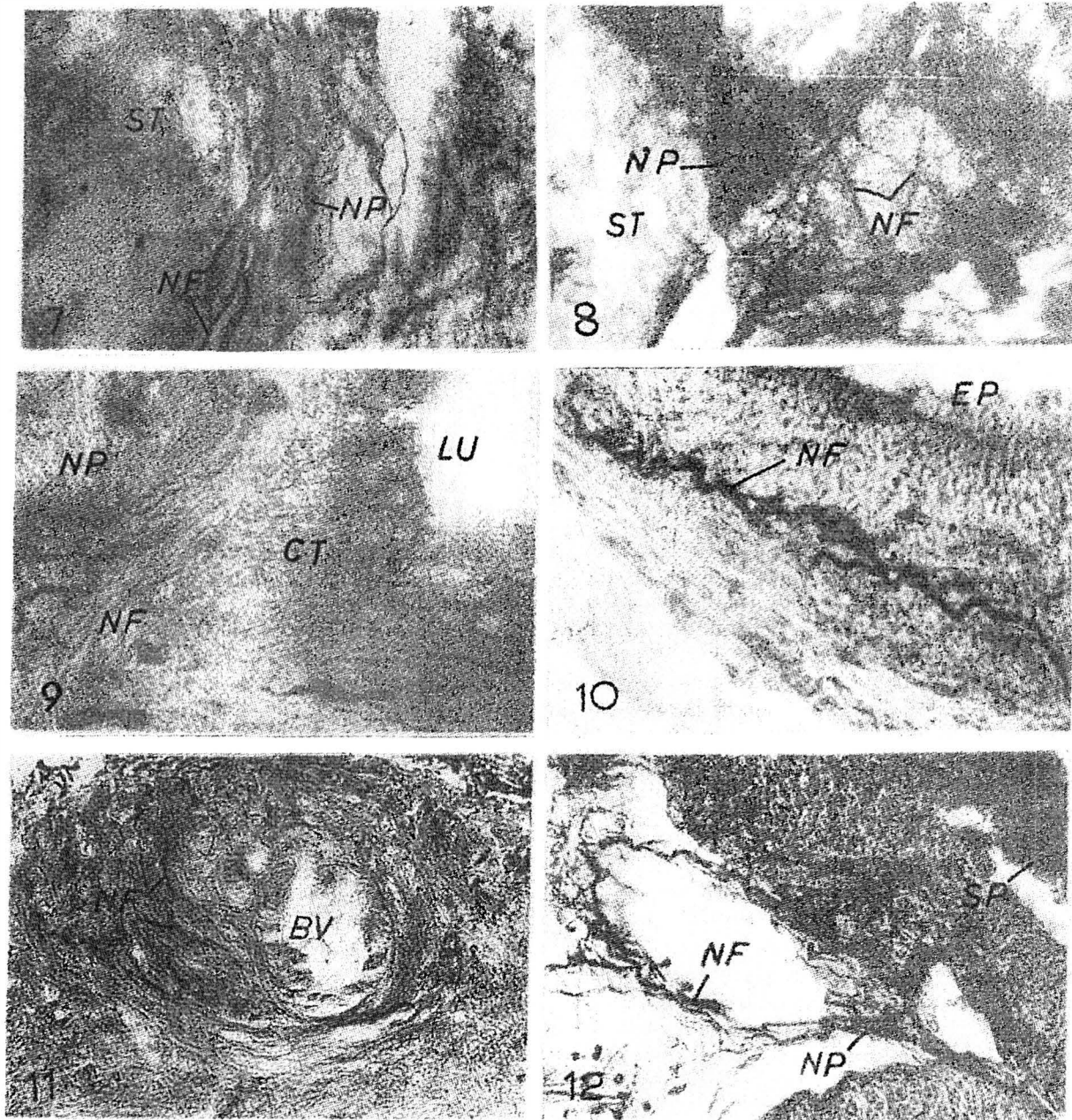
PLATE 2

Fig. 7   Thick nerve fibres (NF) penetrating the tunica propria. Nerve plexuses (NP) are also present. Note the inactive stage of the seminiferous tubule (ST).

Fig. 8   Network of nerve fibres (NF) in the intertubular tissue. Note nerve plexuses (NP) around the seminiferous tubules (ST).

Fig. 9   Nerve plexuses (NP) and many thick nerve fibres (NF) in the connective tissue (CT) of epididymis. Lumen (LU).

Fig. 10   Nerve fibres (NF) near the epithelium (EP) of epididymis.

Fig. 11   Short, thin nerve fibres (NF) around the blood vessel (BV) in the epididymis.

Fig. 12   Nerve fibres (NF) and nerve plexuses (NP) in between the ductules of epididymis. Note the sperm (SP) present in the luman of the ductule.

There was no positive staining of the nerve fibres when the butyrylthiocholine was used as the substrate.

The intrinsic nerve supply to the testis changes according to the changes that occur in the histology of the testis. During August, in the testis of the spermatogenically active stage, shrunken intertubular spaces are present. During this period, a clear-cut association of nerve fibres either with vessels or with Leydig cells can not be established. An individual fibre occasionally passes for some distance within the tunica propria, but it always emerges without penetrating the full thickness and without branching (Fig. 5). However, in the months of October-November, after the release of sperms into the epididymis, the intertubular spaces widen and the Leydig cells along with nerve fibres are observed. Most of the nerve fibres are present at the periphery of the tubule (Fig. 6). Rich innervation is observed throughout the winter months. In the month of June, thick nerve fibres are seen penetrating the tunica propria (Fig. 7). In July, a network of nerve fibres can be traced in between the seminiferous tubules (Fig. 8) and some nerve fibres are found penetrating the walls of seminiferous tubules occasionally.

The epididymis of the turtle T. gangeticus is found to be richly innervated throughout its length. Denser innervation is observed in the proximal part of the epididymis than in other parts of the genital tract. Prominent nerve plexus are found in the thick muscular wall of the epididymis (Fig. 9). Some nerve fibres are seen close to the epithelial lining of some ductules in the epididymis (Fig. 10), but there is no evidence of fine branches, or of endings taking a course between the epithelial cells. Thick and thin nerve fibres are observed in the other musculature of the ductules and also around the blood vessels (Fig. 11).

The density of nerve fibres vary from the anterior to the posterior extremity of the vas deferens and the number of these nerve fibres is extremely high in the muscular coats and the blood vessels of the organ.

Acetylcholinesterase-positive activity is seen in the interductular tissue of the epididymal region and in the muscular walls of the vas deferens. Many short cholinergic nerve fibres are observed in the close vicinity of the epithelium of epididymis and vas deferens.

Seasonally, the intervation of the epididymis varies in relation with the breeding cycles. In the breeding season, when the sperm is present in the lumen of the ductule, a rich innervation is noted (Fig. 12). In the months of November and December the innervation of the spermatic duct is sparse and is further reduced during January and February when the ductule is devoid of sperm. But from March onwards the density of innervation increases until it reaches its maximum in July.

DISCUSSION

The autonomic nervous supply to the male reproductive system has been extensively investigated in mammals and excellent accounts are available for brief comparison with the nervous supply of the reptilian reproductive system under study. Bell and McLean (1970) reported that the outer testicular capsule of rat receives both adrenergic and cholinergic motor nerves. Other investigators have detected a number of nerves in the tunica albuginea of man (Gray, 1947) and rat (Davies et al, 1970). In the present investigation, the network of nerve fibres and their endings are observed in the stretch preparation of the tunica albuginea of the testis of the turtle Trionyx gangeticus.

The blood vessels which are innervated by nerve fibres are found to penetrate more deeply into the interior of the testis in cat (Norberg et al, 1967), and man, swan and rhesus monkey (Baumgarten and Holstein, 1967, 1968). As evident from the present study the testis of the turtle is also innervated by a number of nerve fibres which in turn innervate the blood vessels supplying the testis.

Nerves penetrate the tunica propria to enter the cellular portion of the seminiferous tubules (see Hodson, 1970 for review). This is further confirmed in the present investigation. Some nerve fibres occasionally penetrate the tunica propria of the turtle testis. Okkels and Sand (1947) stated that nerve fibres form a nervous contact with Leydig cells. Gray (1947) found that large groups of the interstitial cells were penetrated by one or more nerve fibres and were commonly broken-up into smaller and smaller groups until a single interstitial cell was entirely surrounded by a fibre. In the present investigation, a number of nerve fibres are noticed in the intertubular spaces of the turtle testis. However, the relationship with these cells depends on their position. Peripheral groups of Leydig cells are associated with many nerve fibres while those in the interior of the testis are associated with very few.

As the Leydig cells are the main source of the production of androgens in the testis (Lofts, 1968), these cells might be regulated directly by the nerve endings (Okkels and Sand, 1940) and indirectly through the blood vessels which were accompanied by the nerves (Kuntz, 1919; Gray, 1947). These blood vessels are particularly provacative with respect to the action of androgen in maintaining and initiating spermatogenesis (Muller, 1957). In supporting the above views, many nerve fibres in close association with the blood vessels are observed in the interstitial tissue of the turtle testis. The Leydig cells are also supplied by these nerve fibres. Nerve endings noted near the Leydig cells strongly support the idea of an involvement of the autonomic nervous system in the regulation of Leydig cell activity.

Unsicker (1975) mentioned that the nerve fibres can more easily be encountered in juvenile animals than in adults, perhaps owing to the smaller volumes of testis, the smaller diameters of seminiferous tubules and large intertubular areas of immature animals compared to mature specimens. He also stated that the amount and distribution of adrenergic nerve fibres varies considerably both in various species and in various stages of the reproduction cycle. Groups of Leydig cells supplied by sympathetic nerve fibres were described as occurring in a testis with low spermatogenic activity in the swan (Baumgarten and Holstein, 1968) in the

pigeon (Ljunggren, 1969) and in the cock (Tingari and Lake, 1972). Ljunggren (1969) considered that there were more adrenergic fibres in the regressed testis of the pigeon than in the testis actively producing spermatozoa. In the present investigation, the intertubular spaces of the turtle testis contain many nerve fibres and their distribution varies during breeding cycles. A number of nerve fibres associated with Leydig cells are observed in the intertubular spaces of the testis during the non-breeding season but during the active breeding period their number is very small. The present findings are in close conformity with those of Ljunggren (1969).

In the present study, silver staining procedures revealed richer innvervation to the inner epithelium and the muscular coats of the epididymis than the cholinesterase technique. The density of innervation varies in different regions of the entire reproductive tract. Innervation in the vas deferens is sparse compared to that in the epididymis. Nerve fibres at the base of the epithelial lining may control the secretion of epithelial cells.

El Badawi and Schenk (1967) consider that the variation in innervation of the parts of male genital ducts are due to differences in both structure and function and they consider that an innervation is necessary for rapid conduction over long distances. As passage of spermatozoa is rapid from the testis to the epididymis, an innervation is necessary in cat and dog when the ductuli efferentes are long. However, Risley (1963) stated that as transportation through the corpus epididymis takes several days an innervation is unnecessary. There is some evidence, traced from the results of a histological study, that in the turtle there is a rapid passage of spermatozoa from the testis to the vas deferens via the epididymis (Rao, 1982) and thus the innervation is considered to be essential to enable spermatozoa to reach the ductus deferens quickly during seminal emission. Rich innervation noted during peak reproductive activity also suggests that the autonomic nerves do play a key role for the propulsion of seminal contents in the excurrent ducts.

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WEIGHT AND MEASUREMENT DATA ON THE GROOVED TORTOISE *TESTUDO SULCATA* (MILLER) IN CAPTIVITY

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INTRODUCTION

The relationship between linear dimensions and weight is of prime importance in biological studies since it yields valuable information on the general well-being and growth rates of individuals, populations and species. This relationship has been studied in several species of Chelonia including *Testudo* (=*Geochelone*) *sulcata* (Cloudsley-Thompson, 1970), *Testudo hermanii* (Jackson, 1978, 1980; Lawrence, 1981; Meek and Inskeep, 1981; Stubbs, Hailey Tyler and Pullford, 1981). *Testudo graeca* (Jackson, 1978, 1980 and Lawrence, 1981), *Chrysemys* (=*Pseudemys*) *scripta elegans* and *Emys orbicularis* (Lawrence 1981 and Meek, 1982).

Meek (1982) quantified the relationship between length and weight and produced a single mathematical formula for each of the above species (*T. sulcata* not included) as well as a comprehensive equation obtained by combing all data sets, in the form of an allometric equation which can be used to compare growth relationships between species or populations.

The work reported here compares the relationship between shell-length, body weight and some linear measurements in two populations of captive *T. sulcata* Miller.

MATERIAL AND METHODS

T. sulcata held in captivity in the Sudan Natural History Museum (Group A) and Khartoum (Group B) were used in this study. For each individual the total weight was recorded to the nearest gram. The shell length (carapace length) from the notch in the nuchal scute to that in the supra caudal scute, shell height and shell width (measured at the point of greatest diameter) and head length were measured to the nearest mm.

RESULTS

RELATIONSHIP BETWEEN LENGTH AND WEIGHTS

According to Meek (1982) the shell length of a chelonian is related to its weight in accordance with the following equation:
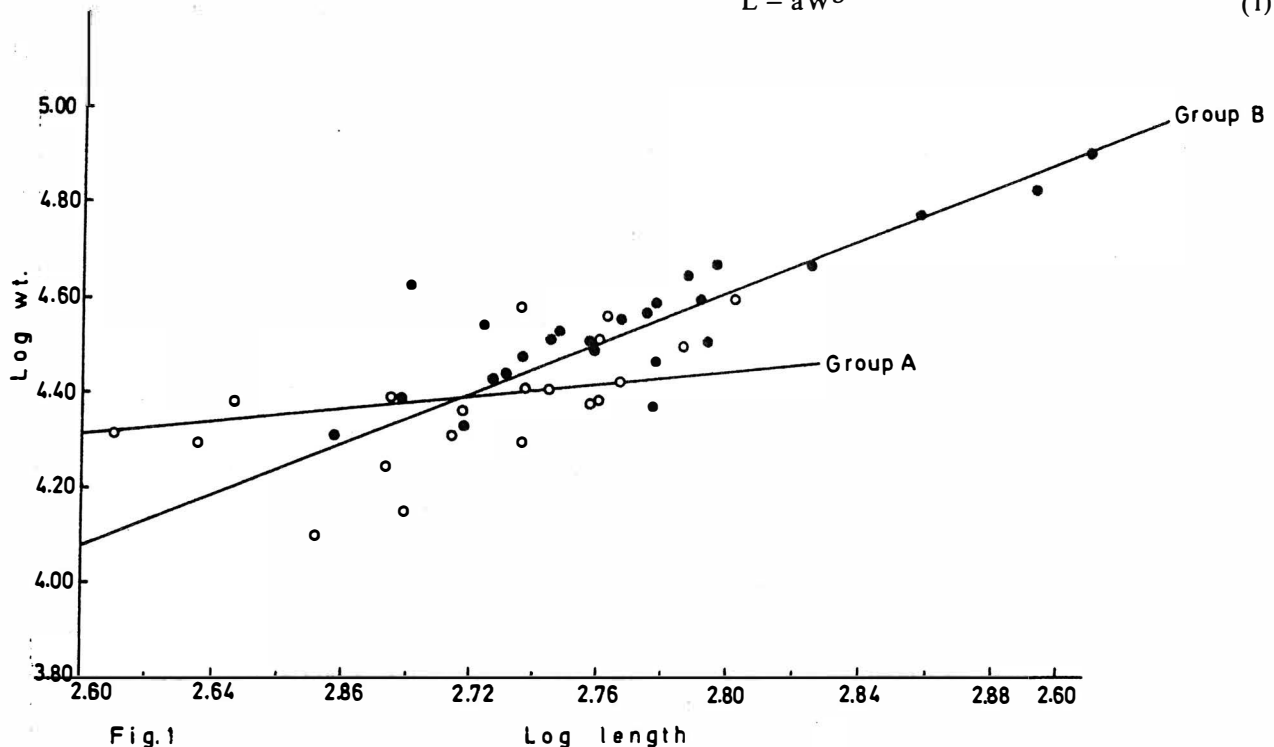
$$L = aW^b \qquad (1)$$

Fig. 1   Logarithmic relationship between shell length and weight in *T. sulcata*. The symbols are (o) for Group A and (●) for Group A and B.

Where

L = shell length in mm, a = the intercept and b an exponent of the mass W in g. The reliability of using shell length in standard growth measurements of *T. sulcata* was tested by plotting the shell length against weight for the two groups. For Group A this gave,

L = — 18.4748 $W^{0.815}$ (r = 0.671, n = 22)

and for Group B

L = — 62.7605 $W^{1.6674}$ (r = 0.935, n = 25)

While group A showed a poor correlation (r^2 = 0.45), group B showed a good correlation (r^2 = 0.86).

Analysis of data following the logarithmic form of Equation 1,

Log L = Log a + b Log W   (2)

yielded points lying about straight line (Fig. 1) and when regression was calculated, the two parameters were found to be related to each other by the following regression equations (Table 1).

Log L = 0.815 Log W — 18.4748 for Group A and

Log L = 1.6674 Log W — 62.7603 for Group B.

The correlation significance (r) was assessed for n-1 degree of freedom and it was found that in both groups r is significant. This is indicative of the reliability of the equation which was a good fit for Group B (r^2 = 0.86) as compared with Group A (r^2 = 0.45) suggesting some change in the two parameters during growth in Group A. This is true in view of the fact that weight increased relatively more than length in Group A than it did in Group B, which showed a higher exponent than Group A. As the value of the exponent b (the regression coefficient) was less than 3 in both groups it was concluded that growth is allometric in *T. sulcata*.

Species	No.	Exponent b	Regression equation Log L = Log a + b Log W	Size range g	Reference
T. gracea	28	0.30	Log L = 2.43 + 0.30 Log W	78-2381	Meek, 1982
T. hermanii	9	0.35	Log L = 11.87 + 0.35 Log W	796-2198	Meek and Inskeep, 1981; Stubbs *et al* 1981
C. scrupta	26	0.36	Log L = 15.25 + 0.36 Log W	25-1276	Meek, 1982
E. orbicularis	7	0.41	Log L = 10.84 + 0.41 Log W	60-595	Meek, 1982
T. sulcata	7	0.91	Log L = 0.91 Log W — 20.6844	3500-42600	Cloudsley-Thompson, 1970
T. sulcata	22	0.81	Log L = 0.81 Log W — 18.4748	12400-39100	Present work (Group A)
T. sulcata	25	1.66	Log L = 1.66 Log W — 62.7603	21000-80000	Present work (Group B)

TABLE 1: Results for the regression analyses of linear relationship between shell length (mm) and body weight (g) in different Chelonian species.

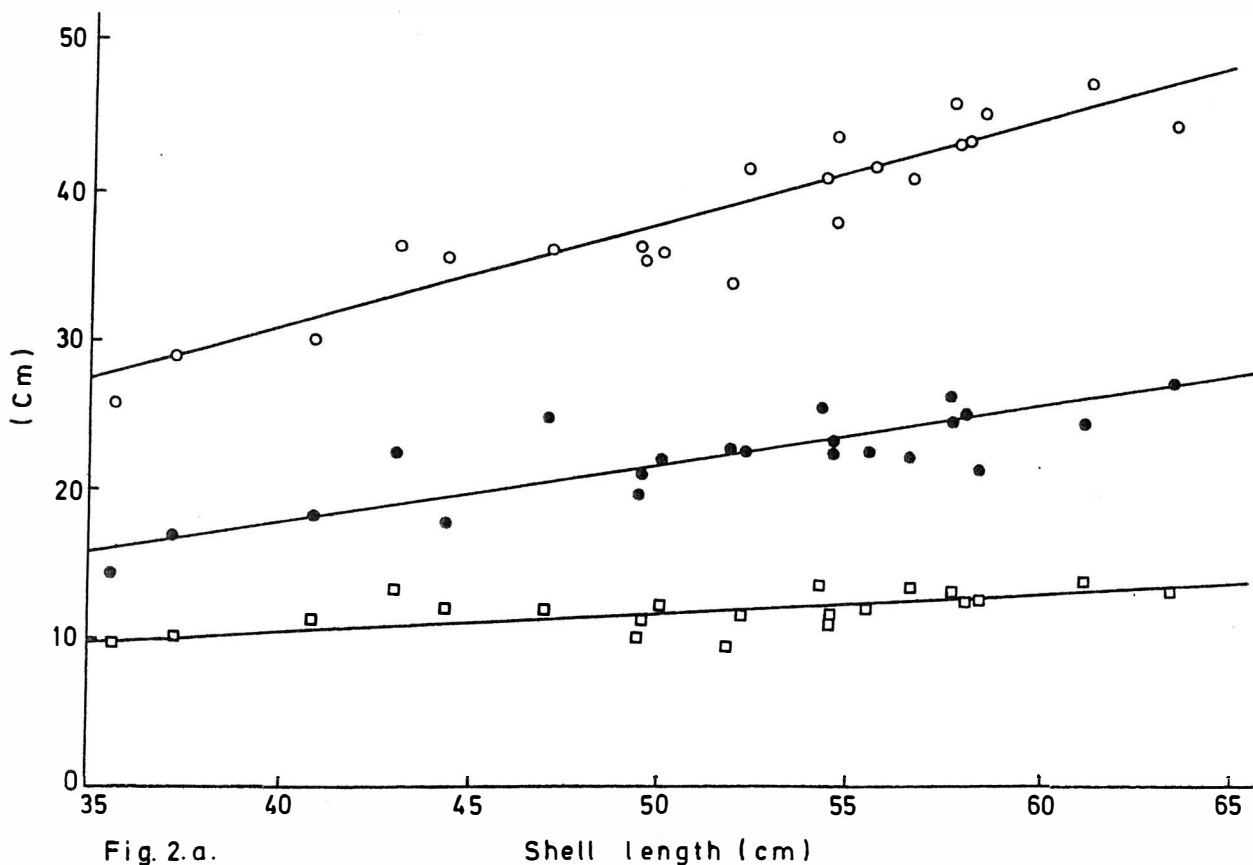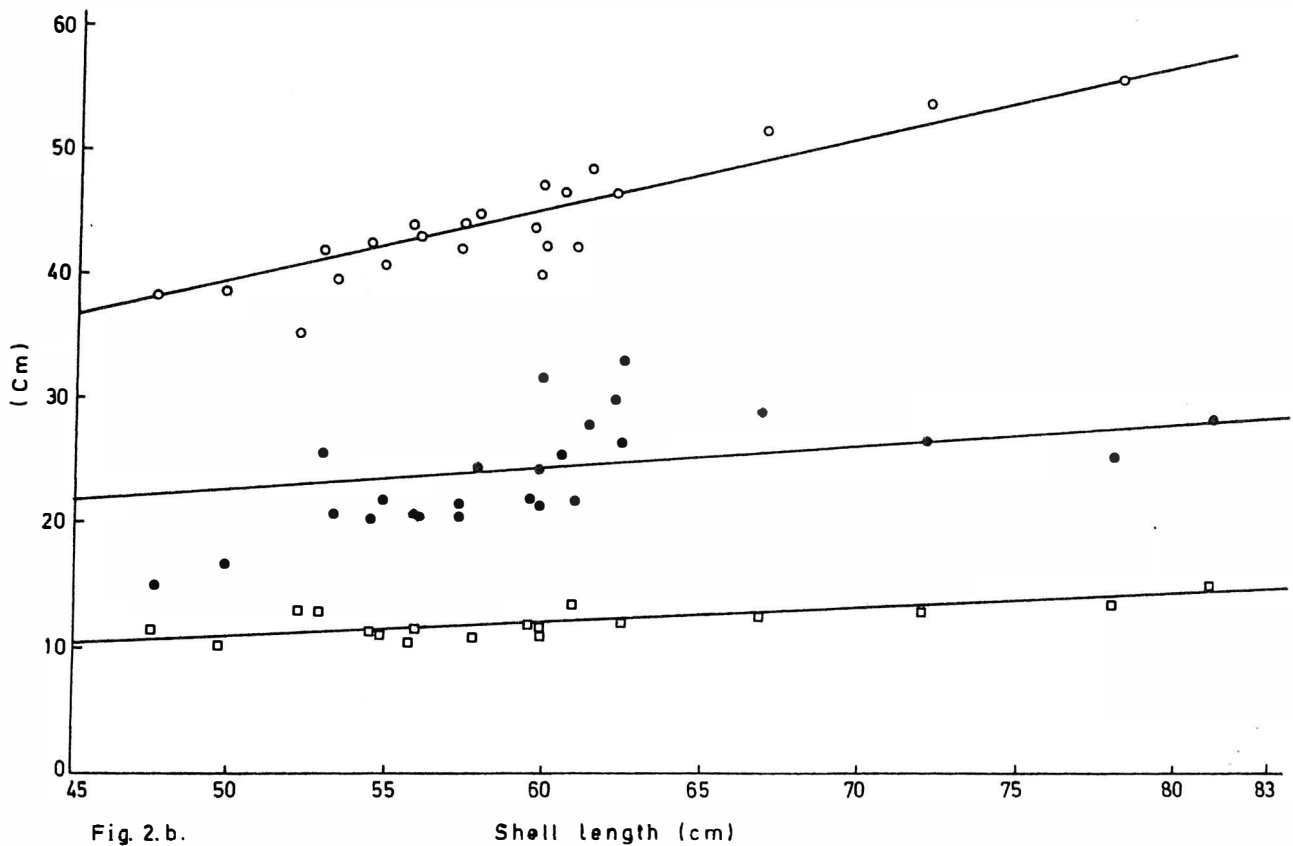Fig. 2.a.   Shell length (cm)

Fig. 2.b.   Shell length (cm)

Fig. 2 Relationship between shell length and shell height (●) shell width (o) and head length (□) in *T. sulcata*. Fig. 2a (Group A) and 2b (Group B).

Source*	Intercept (a)	Regression coefficient (b)	Regression Equation Log X = Loga + b Log L	Correlation coefficient (r)
			GROUP A	
SL/SH	7.27	0.29	Log X = 7.27 + 0.29 Log L	0.71
SL/SW	4.21	0.67	Log X = 4.21 + 0.67 Log L	0.90
SL/HL	7.38	0.09	Log X = 7.38 + 0.091 Log L	0.46
			GROUP B	
SL/SH	3.65	0.33	Log X = 3.64 + 0.33 Log L	0.57
SL/SU	3.65	0.64	Log X = 5.84 + 0.64 Log L	0.83
SL/HL	4.33	0.21	Log X = 0.21 Log L — 4.33	0.29

TABLE 2: Results for the regression analyses of linear relationship between shell length (mm) of *T. sulcata* and some morphometric dimensions (mm).

* SL (shell length), SH (shell height), SW (shell width), HL (Head length).

RELATIONSHIP BETWEEN BODY-LENGTH PROPORTIONS

When the relationships between shell length and other body proportions were tested using regression analysis (Equation 1) in its logarithmic transformation for a straight line relationship (Equation 2) using X instead of W as a morphometric parameter in mm (Fig. 2, Table 1). It was found that the shell height, width and head length all grew relatively slower than shell length. The grooved tortoise tended, therefore, to become longer and flatter with relatively smaller heads.

DISCUSSION

The main findings of the present work and of published data is derived from regression analysis. The study showed that the two groups of captive *T. sulcata* exhibit allometric growth. Cloudsley-Thompson (1970)

demonstrated a close correlation between shell length and body weight in *T. sulcata* but did not quantify the relationship. However, from his data the following regression equation was calculated:

$\text{Log L} = 0.9106 \text{ Log W} - 20.6844$ ($r = 0.9611$, $n = 7$)

This equation, which was a good fit to the data ($r^2 = 0.94$) is indicative to allometric growth and is closer to that shown in Group A (see Table 1).

The exponents for *T. sulcata* are higher than the exponents given for other tortoises (Table 2). According to Meek (1982), lower exponents are indicative of a relatively greater increase in body weight in relation to increase in shell length. Such differences in growth rates between species or populations might be attributed to differences in quantity and quality of food and/or climatic factor. But these remain to be investigated, as does any relationship with reproductive activity and age.

The growth in other morphometric dimensions was investigated against shell length and showed varying degrees of correlation (Table 1). The coefficient of determination (r^2) indicates that predictive equations (Table 1) are good fit for shell length and shell width relationship for both groups. This agree well with the calculated relationship for wild *T. sulcata* from the data given by Cloudsley-Thompson (1970).

$\text{Log L} = 0.7658 \text{ Log X} - 0.3583$

($r = 0.97$, $r^2 = 0.94$, $n = 7$)

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ROUTES AND SPEED OF MIGRATING TOADS (*BUFO BUFO* L.): A TELEMETRIC STUDY

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ABSTRACT

Eleven toads were tracked telemetrically during migration to and from the spawning site. Routes were established. No differences in speed could be detected between males and females or during migration to and from the spawning site. Mean speed was about 30 metres per hour. Speed is influenced (from 22.8 to 49.8 m/h) by the type of vegetation.

INTRODUCTION

Moore (1954) investigated the speed with which *Bufo bufo* migrates from its hibernation site to the spawning site. He followed migrating toads with the aid of a torch and mainly on roads. Apart from the possible disturbance caused by the nearby presence of the investigator, the fact that toads were followed only on roads might give (as is suggested by Moore himself) a biased picture of the mean speed of migration.

Van Nuland and Claus (1981) described a radiotelemetric method with which toads can be traced. Using this method, it is not necessary to follow an individual toad continuously, as it can be traced at any moment. Furthermore, it is possible to keep a relatively large distance between observer and toad and to trace the toad even when it is covered by vegetation.

Using this telemetric method, we investigated the migration of five toads before spawning and seven toads after spawning in spring 1981.

MATERIALS AND METHODS

This study was carried out in the National Nature Reserve 'Overasseltse en Hatertse vennen', situated at 5° 48′ E. long. and 51° 48′ N. lat. in the province of Gelderland, the Netherlands. The area consists of afforested sand dunes with a number of fens. The 'Roelofsven', one of these fens, is a breeding site of the common toad, *Bufo bufo* (Fig. 1). This fen, in origin oligotrophic, is eutrophicated by agricultural activities in its surroundings. For a detailed description of the area see Strijbosch (1976).

To track the animals we used a slightly modified CVN-3 transmitter-receiver unit, as described by Van Nuland and Claus (1981). The energy source of the transmitters consisted of two AgO batteries (Ucar professional 392). The transmitter was glued down to a harness of latex; the toads carried these harnesses on their backs (see also Van Nuland and Claus, 1981). Unfortunately, it appeared that the toads were able to throw off the harnesses, especially in the water. As each transmitter had a distinctive transmitting and pulse frequency (between 120 and 126.5 MHz and 2 and 9 Hz respectively), each toad could be recognised in the field without disturbance.

On the batteries of each transmitter a 2 x 5mm piece of reflecting tape had been mounted. By this we aimed to recognise the toads from long distances with the aid of an infrared lamp and spy-glass. Usually, however, the vegetation inhibited this method and on these occasions cross-bearings were taken. We tried to keep the distance between observer and toad more than 5 metres. At a distance of about 10 metres the accuracy of tracing by taking cross-bearings is smaller than within one square metre.

From sunset onwards all toads were tracked about once an hour. If they did not move at all between about three subsequent observation times (or less, if weather conditions were very unfavourable for the toads), the observations were stopped that night. If at least one toad had moved, observations were made on all animals until no displacements were recorded. The shortest period between two observations was 30 minutes, the longest 90 minutes.

Continuous recordings were made of air temperature, 20cm above ground, humidity and rainfall at a fixed place in the study area. In addition, at each observation of a toad temperature was measured at the surface of the ground and 5cm below as well as 10cm above it with an electric temperature equipment (Wallace EP-400). The temperature was measured at a spot as similar as possible to the spot where the toad was found, keeping the distance between observer and toads as small as possible without disturbing the toad.

As soon as migrating toads were observed during early spring, four toads were collected at a distance of about 600 metres to the 'Roelofsven' (at the Blankenbergseweg, see Fig. 2) and one at a distance of about 100 metres. These toads were tracked on their way to the breeding site. To follow landward migration, six other toads were collected in the neighbourhood of the 'Roelofsven' shortly after the spawning season. Evaluating the data, we assumed that a toad walked in a straight line between two subsequent observations.

RESULTS

Migration to the fen was observed between 8th March and 31st March; migration from the fen from 28th March up to early June. Spawning occurred between 15th March and 30th March.

The routes covered during spawning migration are shown in Fig. 2. Females 2 and 20 reached the 'Roelofsven' in the third night of tracking, migrating in an almost straight line. In the fen both toads very soon lost their harnesses. Males 8 and 14 lost their harnesses under dense vegetation before reaching the fen. Toad 8 obviously did not migrate to the spawning sites in the 'Roelofsven'. Just before male 12 reached the fen it was replaced at the spot where it was caught. That night it walked another 25 metres in the direction of the 'Roelofsven'. The next night it changed its direction and started landward migration (see also Fig. 3). Another 6 toads were tracked during their landward migration (Fig. 3). Migration was considered to have ended if a toad left its hiding place and returned to that place during at least three favourable nights. The end of the landward migration route, being the summer quarter, could be established for 4 toads, viz. males 5, 9 and 12, and female 8a.

We made observations during 27 toad nights (if e.g. 3 toads migrated during one night this is regarded as three toad nights). Only twice was the distance covered during one toad night less than 15 metres (viz. 4 and 14 metres). The maximum distance covered during one toad night was larger during migration to the spawning site than during landward migration. The four largest values were 440, 399, 361, 319 metres and 290, 118, 113, 89 metres respectively. We got the impression that if during the night weather conditions (humidity or temperature) became worse, toads searched for a forest or (in any case) a bush to hide.

Data on the speeds of movements are summarised in Table 1. No significant differences were apparent between sexes or between migration to and from the fen.

It was possible to pick out those observation periods during which a toad migrated through only one 'vegetation type'. We distinguished between forest, grassland and open field. 'Forest' here includes places with trees and a little bit or much ground cover as well as coppice strips and dense bushes; 'open field' includes forest paths, (asphalt) roads and arable land (without vegetation during early spring). In Table 2 all data (male-female, to and from the fen) are lumped together.

Testing statistical differences in mean speed between vegetation types, it is necessary to compare at least the data of six different animals observed in more than one vegetation type (rank sign test, using the mean of the data). With our data we could test in this way only the difference between forest and grassland. The speed in grassland appeared to be significantly higher ($p < 0.05$). The highest speed was observed in a female which moved 61 metres during 30 minutes in open field.

DISCUSSION

The method of fixing the transmitter to the toads seems not to interfere with their activity, as was established by direct observations of toads in their summer habitat as well as in a great vivarium (Aarts, 1982). In our opinion the method is also applicable to migrating toads. It appeared, however, that toads were able to throw off the harnesses in the water and in brambles. This made it impossible to get information about the duration of the stay in the water, the activity pattern during that period and the fidelity to a certain route of migration.

Little information is available in the literature about the migration routes of individual toads. In this study toads migrated in a straight line to their spawning site, neither avoiding nor preferring a special type of vegetation. At daybreak, however, toads preferred a forest (or at least a bush) to hide in at daytime. There they might be better capable of withstanding a sudden period of frost than in the open field (as supposed by Heusser, 1968). Toad nr. 8 did not migrate in a straight line to the 'Roelofsven'. Perhaps it was migrating to another spawning site situated about 300 metres north of the 'Roelofsven'.

Heusser (1968) states that landward migration proceeds at a faster rate than migration to the spawning site. Toads reached their summer quarters soon after the spawning period, having there an

		Migrating to the fen				Migrating from the fen		
	nr.	n.	x̄	s.d.	nr.	n.	x̄	s.d.
Males	8	31	34.9	15.2	9	6	26.7	13.4
	14	10	39.9	18.9	5	4	37.9	12.1
	12	3	24.7	14.9	12	9	30.7	11.1
					7a	11	19.2	19.7
Females	2	15	42.0	33.6	8a	10	50.0	36.0
	20	8	27.6	11.5	15	2	16.0	5.7
					6	9	23.7	16.7

TABLE 1: Mean speed of male and female toads during migration to and from the spawning site. nr. = toad identifier; n. = number of periods in which the toad concerned was observed; x̄ = mean speed of the toad (in m/h); s.d. = standard deviation.

inactive 'latency period' of 2-3 weeks before initiating summer activity. We observed that landward migration was less directional than migration to the spawning site. On 25 out of the 27 toad nights it was raining or raining was stopped just before. As a result long periods of inactivity were observed between short periods of migration. The total period of landward migration, beginning after spawning (late March) up to reaching the summer quarters (early June), was much longer than the period of migration to the spawning site (8th-30th March). Perhaps the discrepancy between our results and those of Heusser can be explained by differences in climate with a longer change-over from winter to summer in the Netherlands as compared to Switzerland. It must be emphasised, however, that during several nights after spawning the toads did not migrate whereas weather conditions were much better than during migration to the fen.

	N.	n.	$\bar{x}$	s.d.
Forest	9	34	22.8	7.1
Grassland	6	23	36.7	9.8
Open field	8	20	49.8	14.5

TABLE 2: Mean speed in m/h ($\bar{x}$) and standard deviation (s.d.) of toads migrating in different vegetation types (see text). N. = number of different toads observed; n. = number of observation periods.
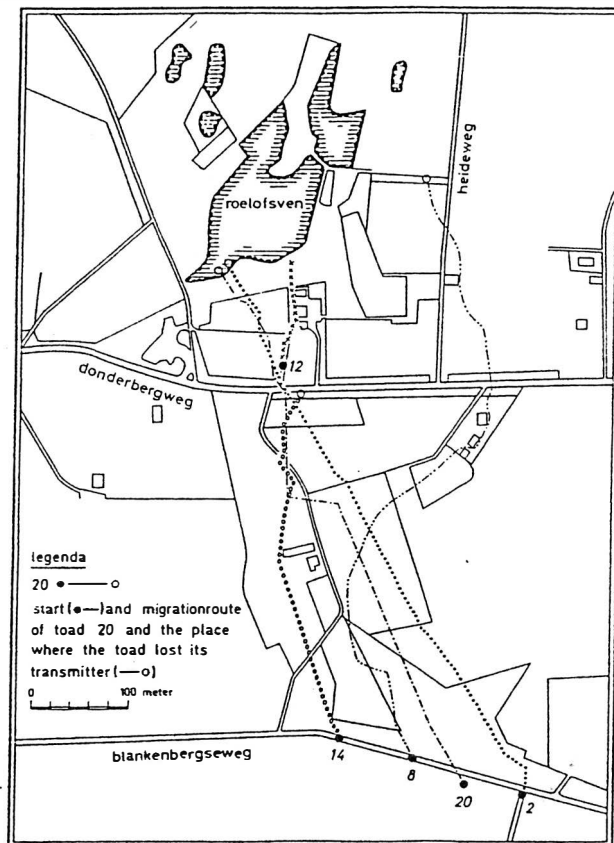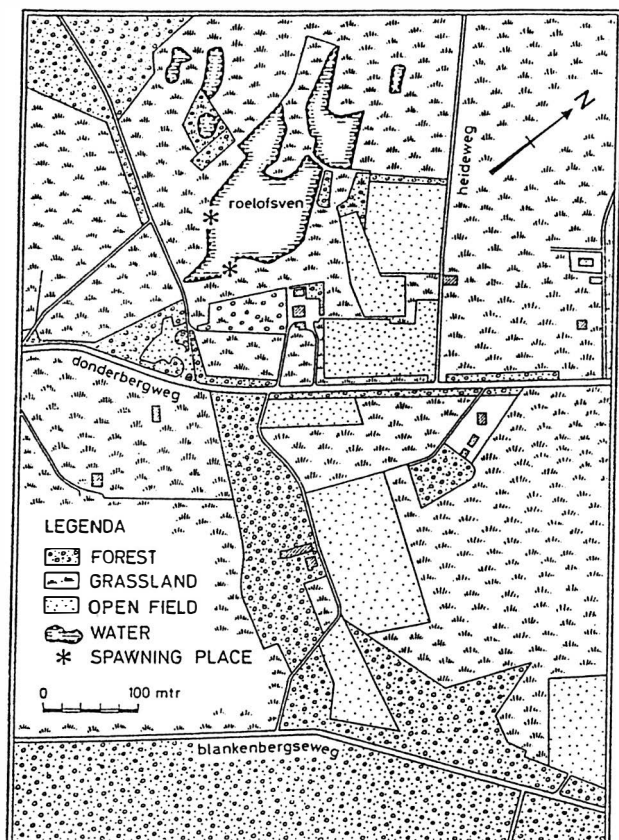

Fig. 1 Survey map of the area. Forest includes dense bushes and coppice strips; open field includes forest paths, (asphalt) roads and arable land (without vegetation at the time of the year).

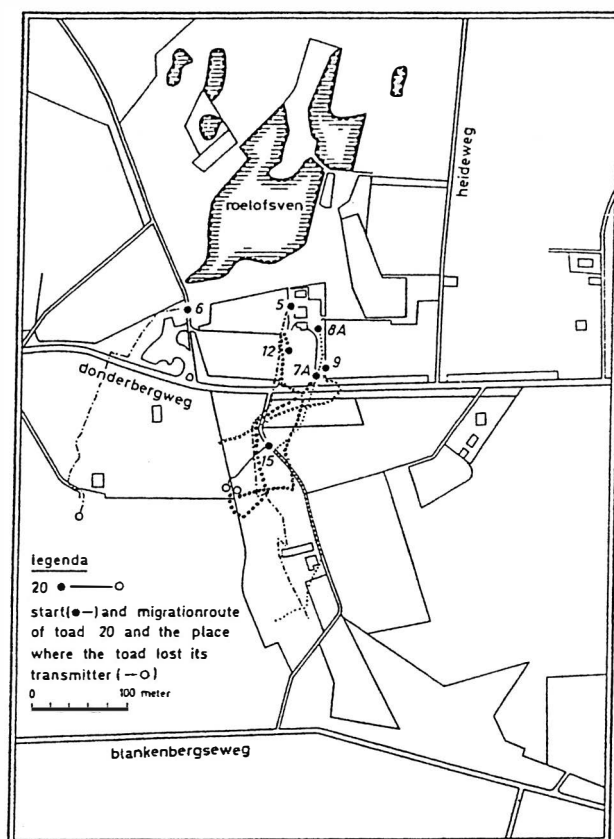Fig. 2 Routes of five toads during migration to the fen.

Fig. 3 Routes of seven toads during landward migration. Toad no. 12 in the Figs. 2 and 3 is the same individual (see text).

There are few data in the literature concerning the speed of migrating toads. Based on 14 specimens, Moore (1954) found speeds of 88-176, 59-122 and 44-88 m/h for males, females and pairs in amplex respectively. He suggested that his results could have been influenced by his method. Every few minutes he traced a toad migrating in open areas (roads, gravelpaths and grassfields) with the aid of a torch. Our data confirm his suggestion that the vegetation influences the speed of a migrating toad. Nevertheless, the speed reported by him is very high, even if compared with our 'open field' data. In our opinion the nearby presence of the investigator might have forced the toads to increase their speed.

Gittins *et al.* (1980) marked toads on their way to the breeding site and recaptured them after a certain period. They state that during one 'activity night' toads migrate between 100 and 250 metres. Oldham (1966) reports that *Bufo americanus* covers a distance of about 225 metres during one night. These data are comparable with ours. This implies that the maximum distance between hibernaculum and breeding site of a toad depends on the number of nights with favourable weather conditions between overwintering and spawning period. For the area studied this number is usually less than six.

Many authors (Kleinsteuber, 1964; Heusser, 1968; Wisniewski *et al.*, 1981) mention threshold temperatures for migration. We could not confirm this as after a very long period with low temperatures, the mean temperature suddenly rose to about 10°C, a value far above the threshold temperatures mentioned. Toads reacted very quickly to these favourable conditions and started the spawning migration; a phenomenon described already by many authors (Jungfer, 1943; Moore, 1954; Kleinsteuber, 1964; Heusser, 1968; Gittins *et al.*, 1980, Wisniewski *et al.*, 1981).

Heusser (1968) and Sander *et al.* (1977) found a correlation between temperature and speed of migration. We did not find such a correlation in the temperature range of 7-14°C. At threshold temperature the speed is possibly lowered, as is suggested by one observation at 4°C of a toad walking only 5 m/h.

Measuring relevant toad temperatures is very difficult. Surface and air temperatures are not precise measures for the temperature of the toad. Therefore we are developing a thermotelemetric system measuring the temperature of the toad itself. We have planned to place thermosensitive transmitters in the abdominal cavity of the toads, enabling us to follow the same toad during its migration to the fen, its stay in the water as well as its landward migration.

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WATER LOSS FROM *TRIONYX TRIUNGUIS* EGGS INCUBATING IN NATURAL NESTS

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(Accepted 27.11.85)

ABSTRACT

In Israel, the oviparous softshell turtle *Trionyx triunguis* lays its eggs in nests buried in elevated sand bars along the banks of the Alexander river. We measured the temperatures and humidity prevailing in natural nests throughout the entire incubation period (78 days), and found that the eggs' hatchability was dependent upon the substrate wetness. In dry sand (water content 0.11 per cent, water potential –2760 kPa), the eggs lost an average of 31 per cent of their initial mass and failed to hatch. In a wetter substrate, in which the water loss of the eggs did not exceed 15 per cent, the eggs hatched successfully.

INTRODUCTION

Oviparous reptiles lay their eggs either in burrows, crevices or nests dug out in the soil substrate. The eggs are then left to develop unguarded by their parents and, throughout the entire incubation period, they are exposed to the impact of the changing physical environment prevailing in their immediate surroundings. There has been much documentation about the effect of temperature and soil water potential on hatching success (Packard, Taigen, Packard and Boardman, 1981; Packard, Packard, Boardman, Morris and Shuman, 1983). Most of the findings, however, were observed in eggs incubated in laboratories under artificial conditions. In this study we aimed at determining the effect of temperature and, especially, humidity, on the eggs of the Nile softshell turtle *Trionyx triunguis*, which were laid and left to develop in natural nests.

MATERIALS AND METHODS

Today, only one viable population of *Trionyx* has been found in Israel. It inhabits the Alexander river which flows westwards into the Mediterranean Sea. Female *Trionyx* lay an average of 40 hard, calcareous-shelled eggs, in nests buried some 30-40cm deep in elevated sand bars along both sides of the river. The laying season is from mid-May to mid-July, incubation lasts some 10-11 weeks and hatching commences approximately in mid-August, lasting for 2-3 weeks.

Three nests were monitored. One (nest A) was located on the northern side of the river, 20m from the river edge. This south-facing sand bank had an incline of 45°. It was poorly covered with sparse vegetation and thus was fully exposed to the sun's impact. The other two nests (B and C) were located on the southern side of the river in a steeper sand bank with scattered but better vegetation cover (*Artemisia monosperma*). Nest A was found three days after the eggs had been laid. Nest B and C were found at the time of laying. The eggs were carefully removed from the nests and numbered according to their position in the nest. They were weighed, their dimensions were measured and

they were then returned to their original position in the nest.

Temperatures of the nests were measured by calibrated copper-constantan thermocouples which were connected to a portable thermometer Wescor TH65. The thermocouples were placed between the eggs at the bottom, centre and top of each nest. For measuring the water potential of the nest's soil we used ceramic-head probes of a Wescor Dew Point Microvoltmeter HR-33T. The probes were placed together with the thermocouples. Water potential values were obtained either from direct reading of the dew point probes, or by using a previously prepared calibration curve in which water potential values were directly related to the water content of the same soil. Soil samples were taken from the sides of the nests and at different depths adjacent to the nests. They were weighed, oven dried to a constant mass and their water content was determined. Known amounts of water were then added to the dry soil, and the water potential of the mixture was measured with the dew point probes (Horton, Wierenga and Nielsen, 1982). There was a good agreement (±5 per cent) between the two methods.

The nests were measured once a week every four hours throughout a 24 hour cycle. After the first weighing, the eggs of nest A were weighed twice more, 10 and 40 days after being laid. The entire treatment (weighing and returning the eggs to their original position) lasted up to 45 minutes, the physical equilibrium of the nest (temperature and humidity) was restored within the next four hours. The eggs of nests B and C were taken from their nests after 70 days of incubation. They were weighed and incubated in the laboratory during the last seven days in incubation in the same soil substrate as the natural nest at a constant temperature of 30°C.

RESULTS

The initial mass of the 108 eggs of the three nests was 17.82±1.1 g (SD), and their average size 30 x 30mm. The incubation period, 76-78 days, was similar for the three groups as well as for other nests located in the same area. Hatching success, however, was quite

different. It was 99 per cent and 95 per cent in nests B and C, respectively, but only 64 per cent in nest A.

We miscalculated the hatching date of nest A and reached the nest site one day after the eggs had hatched. We found 15 dead hatchlings at various stages of hatching, from cracked eggs up to the stage of a body with only a few pieces of shell attached. Of the 15, seven were identified by numbers. These, and probably all of the eggs that failed to hatch, belonged to the top layer of nest A (Fig. 1). Five of the largest and least-damaged dead hatchlings had a mean carapace length of 33.5mm (32.0 to 36.3mm), whereas that of nest B and C's hatchlings was 38.5 ± 5.2mm (SD).

A comparison among the physical environments of the three nests (Table 1) shows that the temperature of nest A was higher by 1.6 and 0.8°C than those of nests B and C, respectively. However, these temperature differences between corresponding layers exist along the entire depth and not only between the top layers of the nests. Therefore, the relative hatching failure of nest A's eggs cannot be attributed to the temperature differences. On the other hand, the top layer of nest A is 6-7 times drier and its water potential is 4-11 times greater than the corresponding layers of nests B and C, whereas the bottom layers of the three nests are much the same. This indicates that the eggs in the top layer of nest A were susceptible to a much higher rate of water loss.

The rate of water loss was estimated from the mass changes of the eggs. The three weighings of nest A's eggs yielded a linear mass change for each egg. This allowed us to assume a constant rate of daily mass change and to predict the total mass loss of each egg on the day of hatching. Similarly, we calculated the total mass loss of the eggs from nests B and C. Fig. 1 shows that 12 out of the 13 eggs laid in the top layer of nest A, and one or two eggs in the next layer, would have suffered a total loss of 20-54 per cent of their initial mass, whereas those on the bottom might even have gained some water from their surroundings. The average mass loss of the top layer's eggs of nest A (31 per cent) is 14-15 times the total loss of the eggs laid in the top layers of nests B and C. In the bottom layers, however, the mass changes of all eggs are within a comparable range (Table 2).

DISCUSSION

The hatching failure of the top layer eggs in nest A can be attributed to several biotic (e.g. predation, egg-handling) and physical factors. Predation, however, can be excluded since marks of digging or footprints of jackals and mongeese, the most common predators in the research area, have never been seen in the nest vicinity. Also, the extra handling during mid-development of nest A eggs might not necessarily have a pronounced effect on hatching success. Since each egg was weighed and handled in the same manner, handling is expected to affect the entire clutch and not only the top layer eggs. Moreover, of the hundreds of metabolic measurements performed in our laboratory on *Trionyx* eggs, many were done on eggs which were weighed and handled in the same manner and frequently as those of nest A. Hatching success was about 90 per cent (Leshem, unpublished data).
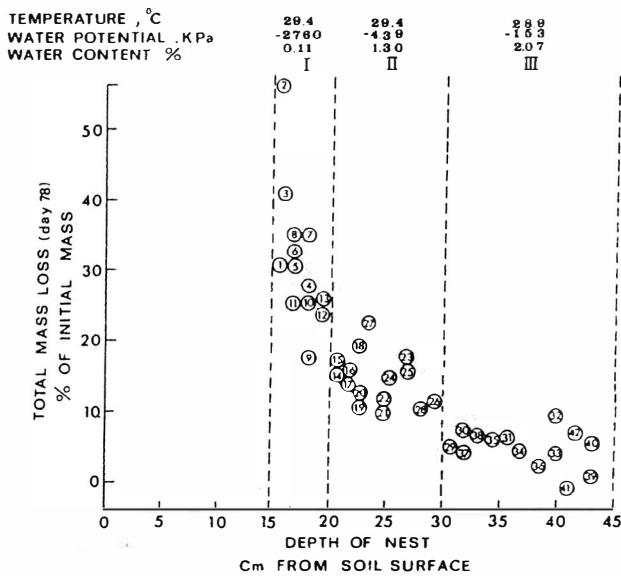

Fig. 1 Nest A. Water losses of *Trionyx* eggs (expressed as % of the initial egg mass) as a function of the depth at which they were buried. Encircled numbers depict the position of individual eggs as they were arranged in the nest when laid. Average temperature and soil humidity conditions at three depths (I, II, III) are given at the top of each layer.

| Nest | Depth of layer from soil surface (cm) | | | | | | | | |
| | 15-20 | | | 25-30 | | | 35-40 | | |
	A	B	C	A	B	C	A	B	C
Water content		0.11	0.62	0.75	1.30	—	—	2.07	1.50	1.00
% of dry sand	±	0.02	0.15	0.15	0.22			0.25	0.30	0.20
Water potential		2760	718	220	439	—	—	153	162	106
–kPa	±	208	85	43	50			62	40	16
Temperature		29.4	27.6	28.6	29.4	27.8	28.4	28.9	27.4	28.2
°C	±	2.9	1.8	1.0	1.8	2.0	1.1	1.6	2.1	1.1

TABLE 1: Environmental variables prevailing in three *Trionyx* nests. Values are mean ± SD.

Apparently, the excessive water lost from the eggs that were laid in the dry upper layer of nest A, was the prime factor determining their hatchability.

Layer depth cm		Nest A*	Nest B	C
15-20		31.1	7.1	1.7
	±	9.6	5.4	4.2
25-30		14.2	2.7	0.5
	±	3.5	1.6	1.2
35-40		4.8	2.0	-0.4**
	±	2.9	1.4	1.4

TABLE 2: Total water loss (% of initial egg mass) of *Trionyx* eggs incubated in natural nests. Values are mean ± SD.

* Predicted values (see text)
** Net gain

The exact mechanism by which reptilian eggs exchange water with their immediate surroundings, whether it is via liquid (Tracy, Packard and Packard, 1978) or via water vapour (Ackerman, Dmi'el and Ar, 1985), has not yet been fully explained. It is known, however, that the rate of water exchange is lower in calcareous shelled eggs than in flexible or leathery shelled eggs (Ackerman *et al.*, 1985). Packard, Taigen, Boardman, Packard and Tracy (1979) and Packard *et al.*, (1981) showed that *Trionyx spiniferus* eggs declined in mass throughout incubation when artificially incubated on substrates of different water potential, and that rates of decline in mass were lower for eggs incubated on wetter than on drier substrates. Our measurements of the carapace length indicate that if the failed-to-hatch embryos of nest A would have hatched, they would be shorter than those of nests B and C. This is in accord with the observation made by Packard *et al.* (1983), that painted turtle eggs exposed to dry substrate produced shorter hatchlings than eggs associated with wet media. Our findings thus support earlier observations and further emphasise the importance of choosing the appropriate nesting site by the female turtle.

A total water loss of about 15 per cent (Fig. 1 and Table 2, centre layers of nest A) during natural incubation is probably the upper line separating hatching success or failure in *Trionyx triunguis* eggs. This value is very similar to that calculated for avian eggs (Ar and Rahn, 1980). The hatching of eggs which are laid in a dry substrate such as the top layer of nest A, would be seriously jeopardised.

ACKNOWLEDGEMENT

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THE FEEDING ECOLOGY OF *PODARCIS ERHARDII* (REPTILIA- LACERTIDAE) IN A MAIN INSULAR ECOSYSTEM

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ABSTRACT

Initial data on the feeding ecology (diet, prey size) of the cycladian wall lizard *Podarcis erhardii* (Reptilia-Lacertidae) obtained during the spring and summer of 1983, is referred to in this report.

INTRODUCTION

Research carried out during the last 20 years by several researchers (Pianka, 1966; Schoener, 1971; Huey and Pianka, 1981) on the feeding ecology of lizards, has helped in understanding predation and foraging modes. During the same period, a great deal of data on the diet of the European Lacertidae was also reported by European researchers (Avery, 1966; Pilorge, 1982; Mellado *et al.*, 1982).

Conversely, research on the ecology and the behaviour of the cycladian wall lizard *Podarcis erhardii*, which differentiates (over 25 subspecies) and predominates in most of the insular ecosystems of the north, central and south Aegean Archipelagos, has been minimal. Only four reports refer to the ecology and behaviour of *Podarcis erhardii* (Gruber, 1971; Gruber-Westrum, 1971; Valakos, 1983; Katsadoracis, 1984), and one on its diet (Quayle, 1983). Quayle's reported data on the diet of the *Podarcis erhardii* resulted from 13 specimens which he collected on September 1983 in the harbour of Ios Island.

The initial data on the feeding ecology of the *Podarcis erhardii* reported in the present study, are from specimens collected every month, from March to July, 1983.

LOCALITIES AND METHODS

Eighty-one specimens (51 males and 30 females) were collected from an insular ecosystem located on the eastern part of Naxos Island (the largest of the Cyclades), 6km south of the small village of Moutsouna. The main characteristics of the area are the rocky terrain, the vegetation, which is maquis, and the intense goat grazing. The most predominant plant species is the *Juniperus phoenicea*; however, *Pistacia lentiscus, Olea europea var. sylvestris* are also abundant. There are also some *Quercus coccifera*.

The lizards were collected with either an airgun or a noose, and the date, time, body length (snout-vent), tail length and weight were recorded for each one. Also every lizard was marked by toe clipping and was fixed in 75 per cent alcohol.

The contents of each stomach were examined under a dissecting microscope and every food item was measured and recorded. In the cases where there were only parts of a food item (impossible to measure) only the name of the food item was recorded.

RESULTS

The types and the number of food items found in the stomachs of the 81 *Podarcis erhardii*, are presented in Tables 1 and 2.

A large number of lizards (both sexes and every month) preferred Coleoptera; hence, the percentage of this prey was high (30 per cent).

The second most important food item in the preference of *Podarcis erhardii* was Orthoptera. Consumption of this prey began to increase after May, and the highest percentage appeared in June (A = 25.7%, S = 66%); however, a smaller percentage was found in female lizards (A = 12%, S = 47%). (A and S are defined in the caption of Table 1.) There was also a high percentage of spiders, which was higher in females during May (A = 16%, S = 100) and June A = 15%, S = 53.3%).

We also noted that there was a high content of prey in some groups of food items only during one or two months due to the fact that there was an abundance of these prey items during specific periods (larvlae of insects, Hemiptera, Orthoptera).

In both sexes, there was a stable contribution every month by some groups of food items (snails, coleoptera, ants). There were also some animals present in the prey which lived under stones or were active only at night (pseudoscorpions, chilopoda).

Lizards prefered prey which had a mean length of about 5mm (Fig. 1). There was no correlation between mean prey length and lizard snout — vent length (r = 0.015). There were no overall significant differences between males and females in the mean length of prey (t = 1.02 p<0.01, Table 3). However, during the months of June and July there were some significant differences between males and females in the mean lengths of prey (t = 3.58 p<0.01, Table 3); whereas, in March, April and May, the differences were insignificant (t = 0.66 p<0.01, Table 3).

Food category	N = 81 n	A	S	N =51 ♂ n	A	S	N = 30 ♀ n	A	S
Gastropoda	34	8.5	33	19	8	33	15	10	33
Spiders	50	12.4	48	28	9.7	45	22	14.5	53
Pseudoscorpions	2	0.5	2.5	2	0.9	4	—	—	—
Harvestmen	3	0.7	2.5	1	0.4	2	2	1.3	3.3
Chilopoda	2	0.5	2.5	2	0.9	2	—	—	—
Coleoptera	124	31	78	77	34	80	47	31	73
Orthoptera	65	16	49	41	18	53	24	16	47
Diptera	10	2.5	11	7	3	14	3	2	10
Hemiptera	24	6	28	5	2	11	19	12.5	27
Ants	30	7	25	16	7	24	14	9	27
Hymenoptera	22	5	19	10	4	16	12	8	27
Mantidae	5	1	5	4	2	6	1	0.7	3
Blattidae	1	0.2	1	1	0.4	2	—	—	—
Lepidoptera	1	0.2	1	1	0.4	2	—	—	—
Neuroptera	1	0.2	1	1	0.4	2	—	—	—
Larvae of insects	28	7	33	12	5	24	16	11	53
TOTAL	402			227			150		

TABLE 1: Food items found in stomachs of 81 (30 ♀, 51 ♂) *P. erhardii* collected from March to July of 1983. The symbols represent: N = number of lizards, n = number of prey, A = % of total number of prey, S = % of lizards containing the food category. (A = number of specimens containing of food category/total number of specimens x 100, S = Lizards containing the food category/total number of lizards x 100).

Food category	March		April		May		June		July	
	A	S	A	S	A	S	A	S	A	S
Gastropoda	13	31	7	30	6	32	9	34	11	34
Spiders	11	31	17	80	17	84	8	31	10	34
Coleoptera	39	62	33	90	33	90	23	68	36	100
Ants	8	23	4	21	8	29	8	22	15	44
Larvae	21	54	14	60	5	37	5	20	4	22
Hymenoptera	—	—	—	—	10	37	6	23	2	11
Orthoptera	—	—	—	—	14	52	26	66	15	77

TABLE 2: Main food items found in stomachs of 81 *P. erhardii* during March, April, May, June, July 1983. A and S as Table 1.

MARCH-APRIL-MAY-JUNE-JULY 1983

	N	n	x (prey)	Sx	t	P
Males	43	219	5.27	3.89	2.02	<0.01
Females	30	183	4.54	3.19		

MARCH-APRIL-MAY 1983

	N	n	x (prey)	Sx	t	P
Males	22	111	4.71	3.17	0.66	<0.01
Females	12	95	4.37	2.27		

JUNE-JULY 1983

	N	n	x (prey)	Sx	t	P
Males	21	108	5.85	4.46	3.58	<0.01
Females	18	86	4.38	3.25		

TABLE 3: Mean prey lengths for male and female lizards during the months: March, April, May, June, July — March, April, May — June, July, 1983, and probabilities of significant differences by t-test. N = number of lizards. n = number of prey. x = mean prey length mm. Sx = s.d. P = probability.

Food category	Podarcis erhardii	Lacerta lepida	Podarcis hispanika	Acantho-dactylus erythrurus	Lacerta manticola	Lacerta viridis	Psamodromus algirus
Coleoptera	29.74	47.6	13.3	33	28.1	60	21.5
Orthoptera	15.6	3	1.7	0.6	3.03	8	8.1
Hymenoptera	5.28	10.8	22	22	8.65	—	7
Ants	7.2	—	—	—	3.03	4	—
Hemiptera	5.75	1.9	13.7	14	5.61	—	18.6
Larvae	7	2.4	5.2	14	—	—	31.4
Spiders	12	0.8	26	8	21.2	—	8.1
Gastropoda	8.15	14.4	—	0.3	—	—	—
Author	Valakos	Escarre	Escarre	Escarre	P. Mellado	Bruno	Escarre
Year	1985	1983	1983	1983	1982	1970	1983

TABLE 4: Food items found in stomachs of some Lacertidae. Numbers are the per cent of total number of prey.
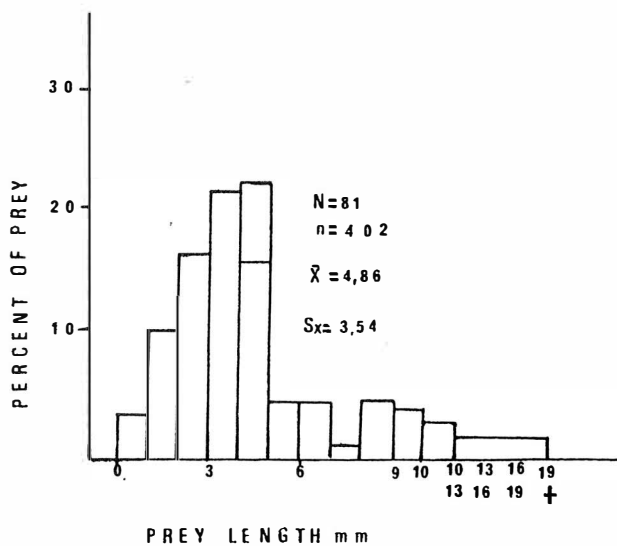
PREY LENGTH mm

Fig. 1   Size frequency of food items. N = number of lizards, n = number of food items, $\bar{x}$ = mean prey length, Sx = s.d.

DISCUSSION

Just as is the case with other Lacertidae of Europe (Table 4), *Podarcis erhardii* feeds mainly on arthropoda. The groups of food items in the prey of *Podarcis erhardii* are almost the same as those of *P. hispanica, Lacerta lepida, Psammodromus algirus, Acanthodactylus erythrurus* (Escarre and Verica, 1983), *L. vivipara* (Pilorge, 1982), *Lacerta* monticola (Mellado, 1982).

The most predominant group in the food of the *Podarcis erhardii* was coleoptera. Coleoptera is also the most predominant group in the food of the lizards referred to in Table 4.

The opinion that ants are predominant in the food of *Podarcis erhardii* on Ios Island (Quayle, 1983) is in contrast with the results of this report; perhaps however, this is because the lizards were collected from the harbour of Ios Island and the number was small (13 specimens). The percentage of ants is small in the European lizards referred to in Table 4. *P. erhardii* is not a completely opportunist feeder because the abundance of some of the groups of food items found was smaller than their abundance in the biotope (ants, hemiptera, diptera). The same preference appears in *Uta stansburiana* (Best and Gennaro, 1984). *Podarcis erhardii* is mainly a widely foraging predator because there were several sedentary animals (snails, pseudo-scorpions, etc.) in its prey and also it used many different types of prey (Huey and Planka, 1981).

Podarcis erhardii preferred prey with a mean length of about 5mm (although it ate prey with lengths up to 20mm). The same lengths of prey are preferred by *Lacerta vivipara* (Pilorge, 1982), as well as by other lizards which have the same length as the *P. erhardii (Sceloporus graciosus* snout-vent length = 60-70mm and x prey = 5mm; Rose, 1976).

The significant difference in mean prey lengths between males and females in June and July probably occurs because, due to the presence of eggs during this time, the females eat small prey as the volume of their stomachs is smaller than that of the males (Valakos, 1983). Many researchers have found that there is a positive correlation between size and prey length, e.g. in *Anolis* (Schoener, 1968). On the contrary, there was no correlation between the size of the *P. erhardii* and the prey length. The same happens with *Sceloporus graciosus and Sceloporus occientalis* (Rose, 1976). Rose assumes that the correlation between the lizard size and the prey size occurs only in the sit-wait predators like *Anolis* (Rose, 1976).

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3. Papers should be concise with the minimum number of tables and illustrations. They should be written in English and spelling should be that of the *Oxford English Dictionary*. Papers should be typed or produced on a good-quality word processor, and double-spaced with wide margins all round. Good quality paper is essential for the top copy. Except for short notes, papers should be divided into sections. The first sub-head will be centred in capitals, the second shouldered in lower case, and the third run on in italics. Footnotes are not permitted.

4. For all papers the title should be followed by the name(s) of the author(s) and the address or name of the Institution in which the work was done. For major papers a short abstract is required before the body of the paper. Acknowledgements should be included before the list of references.

5. The usual rules of zoological nomenclature apply.

6. Tables are numbered in arabic numerals, e.g. Table 1; they should be typed on separate sheets and divided by horizontal lines.

7. Line drawings and half-tones are numbered in sequence in arabic numerals, e.g. Fig. 1. If an illustration has more than one part each should be identified as (a), (b), etc. The orientation and name of the first author should be indicated on the back. They should be supplied for uniform reduction by one-half on A4 size paper to fully occupy the width of the paper. Drawings should be in Indian ink on good quality tracing material, Bristol board or faintly *blue*-lined graph paper; photographic prints may be submitted. For half-tones high quality glossy prints are required. All labelling should be applied to illustrations using stencils or transfers. A metric scale must be inserted in micrographs, etc.; a figure for magnification in the legend is not acceptable. Legends for illustrations should be typed on separate sheets.

8. References in the text should be given as in the following examples: Smith (1964) stated . . ., observed by Smith (1964s, b), Smith & Ones (1963). For three or more authors, the complete reference should be given at the first mention, e.g. (Smith, Jones & Brown, 1972), and *et al.* used thereafter (Smith *et al.*, 1972). For the list of references *the full title or standard abbreviations of the journal must be given*. The following examples will serve to illustrate the style and presentation used by the Journal.

   Bellairs, A. d'A. (1957). *Reptiles.* London: Hutchinson.

   Boycott, B. B. & Robins, M. W. (1961). The care of young red-eared terrapins (*Pseudemys scripta elegans*) in the laboratory. *British Journal of Herpetology* **2**, 206-210.

   Dunson, W. A. (1969a). Reptilian salt glands. In *Exocrine glands*, 83-101. Botelho, S. Y., Brooks, F. P. and Shelley, W. B. (Eds). Philadelphia: University of Pennsylvania Press.

   Dunson, W. A. (1969b). Electrolyte excretion by the salt gland of the Galapagos marine iguana. *American J. Physiol.* **216**, 995-1002.

9. Final acceptance of a paper will depend upon the production by the author of a typescript and illustrations ready for the press. However, every assistance will be given to amateur herpetologists to prepare papers for publication.

10. Proofs should be returned to the Editor by return post. Alterations must be kept to the correction of errors; more extensive alterations will be charged to the author.

11. 25 offprints are provided free of charge. Further copies (minimum of twenty-five) may be purchased provided that they are ordered at the time the proofs are returned.

THE HERPETOLOGICAL JOURNAL

Volume 1, Number 3 December 1986

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